

The Taxonomic Significance of ducts in the corolla lobes of *Vernonia* (Vernonieae: Asteraceae)

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Academic editor: *Peter de Lange* | Received 29 October 2015 | Accepted 4 December 2015 | Published 12 January 2016

Citation: Robinson H, Yankowski S (2016) The Taxonomic Significance of ducts in the corolla lobes of *Vernonia* (Vernonieae: Asteraceae). *PhytoKeys* 58: 1–7. doi: 10.3897/phytokeys.58.7009

Abstract

The multiple longitudinal ducts in the corolla lobes found in the closely related genera *Vernonia*, *Vernonanthura* and *Trepadonia* are microscopically studied and illustrated. The lack of such ducts in the two South American species that have until now been retained in *Vernonia* indicates that they should probably be excluded from the genus.

Keywords

Ducts, corolla lobes, *Vernonia*, *Vernonanthura*, *Trepadonia*

Introduction

The generic concept of the genus *Vernonia* was simple and un insightful for over 150 years from the time of its inception in Schreber (Gen. 2: 541. 1791, nom. cons.), with the eastern North American type *Serratula noveboracensis* L., type cons. *Vernonia* was the core genus of the tribe Vernonieae, having the combination of capillary pappus and non-liguliform florets that were common to all core genera of the Asteraceae during that time. Some segregates were named, such as *Baccharoides* Moench. and *Gymnanthemum* Cass., in Africa, *Eremosia* Gleason in Mesoamerica and *Critoniopsis* Sch.Bip. in South America, but these were not generally recognized at the generic level.

The concept of *Vernonia* began to change in the last 30 years as is partially summarized in the treatments by Robinson for the Paleotropical (1999a) and the American members (1999b) of the tribe. The altered concept reduced the genus *Vernonia* to a restricted group of species mostly directly related to the type species *Vernonia noveboracensis* (L.) Michx., a group with eleven species in eastern North America, ca. 5 species in the highlands of central Mexico, and one eastern North American species reaching the Bahamas. Until now, two species in South America have been retained in *Vernonia*. The genus consisted of species having a cymiform inflorescence with seriate “scorpioid” cymose branches deflected at the nodes, glanduliferous anthers, a somewhat rhizomiform rootstock and echinate weakly sublophate pollen. Closest relatives were considered to be members of the genus *Vernonanthura* H. Rob. with ca. 68 species in tropical America, and *Trepadonia* H. Rob. with two species on the eastern side of the Andes in Peru and western Brazil. *Vernonanthura* differed most notably by the more pyramidal inflorescence with cymiform branches and an often tuberous rootstock, and *Trepadonia* was scandent with widely spreading lateral branches in the inflorescence. The comparative close relationship between *Vernonia* and *Vernonanthura* was reflected fully in the DNA sequence studies of Keeley et al. (2007).

A unifying anatomical structure of the three related genera in the typical element of the tribe Vernonieae is found in the study of the corolla lobes of the group. The corolla lobes of *Vernonia* are filed with multiple parallel ducts containing resin or oils of some type (Fig. 1a–d). These ducts were first noted in the related genus *Trepadonia* H. Rob., and they were illustrated crudely with a photomicrograph in the paper describing that genus (Robinson 1994). Subsequently, during casual observations during systematic work, the ducts were seen in typical *Vernonia* and in numerous species of the closely related *Vernonanthura*. In the latter genus the ducts were often observed in dried specimens under the dissecting microscope. The ducts were represented schematically in the plates of generic characteristics in the study of American Vernonieae by Robinson (1999b).

All initial observations of the ducts were in material mounted in Hoyer’s Solution, and no contents of the ducts were observed. It was when some material was observed microscopically in water mounts that resin or mucilage was seen in the ducts. Given the potential taxonomic importance of the ducts, a first determined effort is made here to provide a proper illustration of the structure.

Methods

Material examined was from dried specimens in the US National Herbarium (US) plus fresh material of *Vernonia noveboracensis* (L.) Michx., the type species of the genus *Vernonia* Schreb., collected on Roosevelt Island and placed in FAA. Herbarium material studied included *Vernonia noveboracensis*, *Vernonanthura brasiliiana* (L.) H. Rob., the type species of *Vernonanthura*, and the two species, *Vernonia echioides* Less., and *V. incana* Less., the latter two species that until the present have been the only South

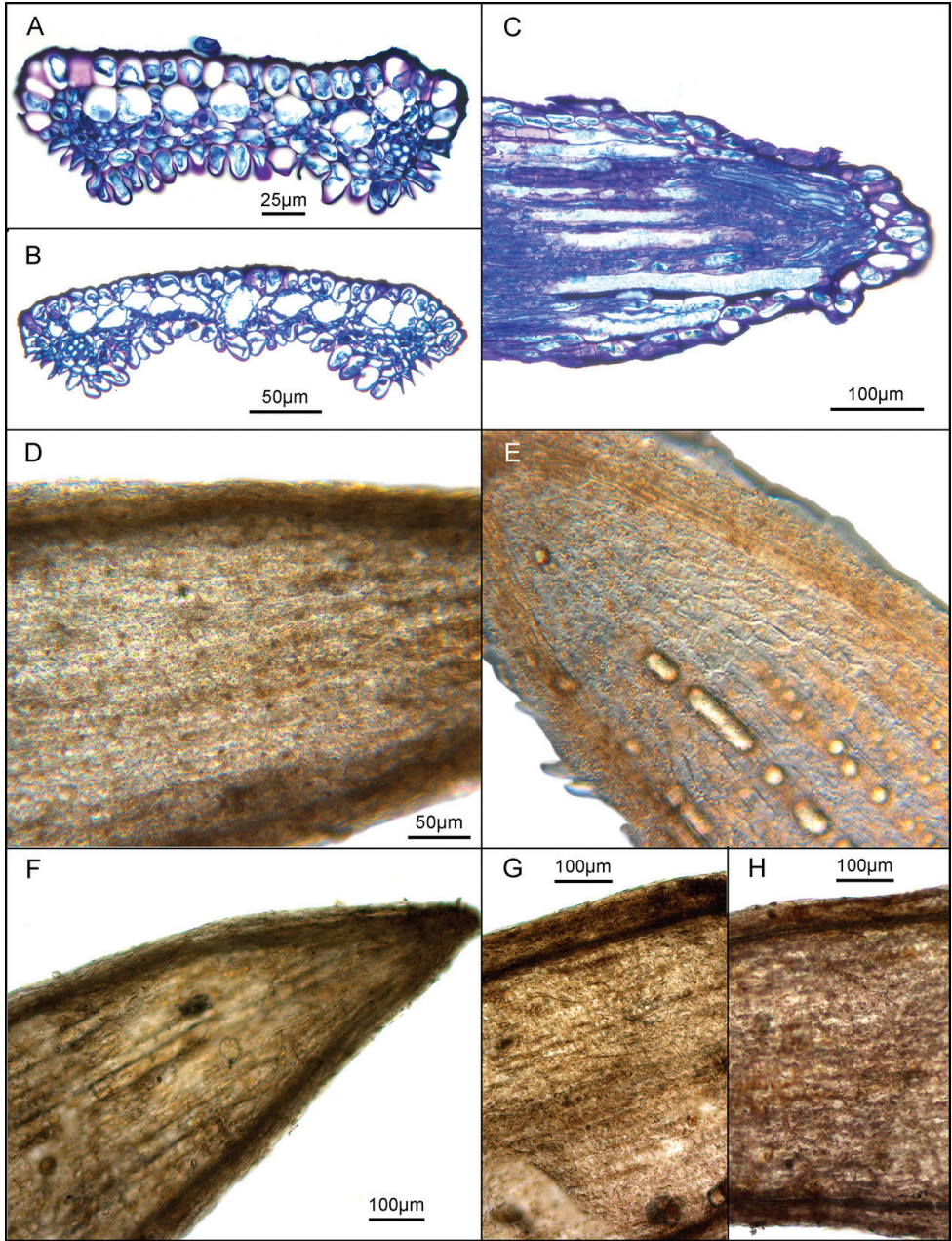


Figure 1. A–D: **A, B,** *Vernonia noveboracensis* cross-sections of corolla lobes, outer surface upward **C** longitudinal section of corolla lobe showing multiple ducts **D** corolla lobe from specimen in preservative showing only poorly defined partitions between ducts **E** *V. angustifolia*, corolla lobe from freshly collected specimen showing fresh resin in ducts **F** *Vernonanthura brasiliiana*, corolla lobe from dried herbarium specimen showing solidified contents of ducts with walls over-lying cell layer **G** *Vernonia echinoides*, part of corolla lobe from dried herbarium specimen showing some short-stalked capitate glands **H** *Vernonia incana*, part of corolla lobe from dried herbarium specimen.

American species retained in the genus *Vernonia*. For purposes of the study, four additional species of *Vernonia* were examined from dried material, *V. acaulis* (Walt.) Gleason, *V. baldwinii* Torr., and *V. blodgettii* J.K.Small all from eastern North America, and *V. karwinskiana* DC. From Oaxaca, Mexico. A final collection was of an unvouchered collection of *Vernonia angustifolia* Michx. from a garden in Arlington, Virginia, and placed directly on a microscope slide (See Appendix for citations).

For purposes of microtome sectioning, living material of *Vernonia noveboracensis* was field collected and fixed in formal-aceto-alcohol (FAA 1:1:18). Flower heads were subdivided, dehydrated with 2-2 dimethoxypropane (DMP) (Postek and Tucker 1976), then infiltrated and embedded in paraffin. Serial sections were made at 5 μ m, stained with buffered Toluidine blue O (Sakai 1973) and mounted in Lipshaw's synthetic mounting resin. Unopened buds were used to avoid the recurved condition of the lobes in opened florets. Placement of bud material in the mounting resin was uncertain since the florets had five lobes that were themselves somewhat curved. Cross-sections were easily obtained. Longitudinal sections were by chance.

For views of unsectioned material, corolla lobes were taken from fixed material and from dried herbarium specimens and one freshly collected specimen for whole mount observation.

Images (photomicrographs) were captured in bright field or Nomarski (DIC) using a Zeiss Standard 16WL microscope, a Zeiss Universal Research microscope or a Zeiss Axiophot equipped with a Retiga 1300i digital camera (Q Imaging Corp.) and an image acquisition and processing system capable of live tiling and live EDF (extended depth of field) by MediaCybernetics/ImageProPlus 7.0.

The material from dried herbarium specimens was remoistened in water and mounted on microscope slides in water to preserve any resin or mucilage that might be in the ducts.

Results

There are two ways of showing the ducts in the corolla lobes of *Vernonia*. One is by sectioning the material, the other is by whole mounts of the corolla lobes placed under the microscope. Both methods have been used here, and both methods have unmistakably demonstrated the ducts.

Cross-sections of the corolla lobes of *Vernonia noveboracensis* clearly show the series of seven to twelve ducts in a lobe (Fig. 1A & B). The ducts are mostly surrounded by individual sheaths of cells, the same cells that form the partitions between the ducts that were obvious in the initial crude studies of the characteristic in *Trepadonia*. A longitudinal section (Fig. 1C) shows the ducts as elongate structures that lack cross-walls. The longitudinal sections of the corollas indicate that the ducts are not completely restricted to the corolla lobes, but that they begin below the lobes, especially along the main veins of the corolla. Both cross- and longitudinal sections show the ducts as

empty; apparently Hoyer's Solution and preservative both completely remove all resin or mucilage contents of the ducts.

The second method of viewing the ducts is the one that showed the structure in the paper describing *Trepadonia* (Robinson 1994). However, that preparation was in Hoyer's Solution and retained no resin or mucilage in the ducts. The new views first used material that had been placed in preservative, and the ducts were also empty. Mounts of corollas in water, however, showed the ducts clearly with their chemical contents, and the presence of material in the ducts made the ducts more obvious.

Figures 1E & F show the lobes of *Vernonia angustifolia* and *Vernonanthura brasili-ana* with resin or mucilage in the ducts. The duct contents show that multiple longitudinal ducts are present in both genera. The resin contents do not seem to appear in all the ducts of any lobe at the same time. The fresh material of *Vernonia angustifolia* obtained from garden plant shows lobe that has neither been dried nor treated with chemicals. Even here, the ducts seem to be only partially filled with resin. Observations of *V. acaulis*, *V. baldwinii*, *V. blodgettii*, and *V. karwinskii* were in water on slides simply to confirm the presence of the ducts in a broader representation of the genus. While the ducts can be seen once the observer is familiar with their appearance, they are not quite obvious enough to be used as anything more than a supplementary key character in taxonomic treatments. The character could be useful in separating *Vernonanthura* from *Critoniopsis* Sch.Bip. in the Andes, and *Vernonanthura* from the adventive *Gymnanthemum amygdalinum* (Del.) Sch.Bip. ex Walp. in Brazil.

The survey of the whole tribe for presence of multiple ducts has not been rigorous, but certainly on a par with the observations that led to the initial discovery of the ducts in *Trepadonia*, *Vernonanthura* and *Vernonia* (Robinson 1994). It remains to be seen what different kind of internal structure occurs in the corollas in other members of the Vernonieae. It can only be said that multiple longitudinal ducts have not been seen in any of the other genera. As an indication other possible specialization, at least one African species, still known as *Vernonia potamophila* Klatt, shows chambers of some kind in its lobes.

The nature of the chemical contents of the ducts remains unknown. The types of chemicals known from the Vernonieae include epoxy resins, but these have been found most notably in genera like *Stokesia* L'Hér. (Gunn and White 1974) and *Centrapalus* Cass. (Purdue et al. 1986, 1989), neither of which has the multiple longitudinal ducts in the corollas. Terpenoids are common in many Vernonieae (Herz 1977; Bohlmann and Jakupovic 1990), but their end products are not tolerated by Insects and Mammals or the primary tissues of the plants in which they are produced. For that reason, in the Asteraceae, the terpenoids are accumulated in special cells usually at the tips of glandular hairs such as those seen on the lobe of *Vernonia echioides* (Fig. 1G). Acetylenes are a stronger possibility, but they are not varied in Vernonieae where only pentaynenes have been reported (Bohlmann et al. 1973). In other tribes such as the Heliantheae, Acetylenes are highly varied and occur in ducts, and where they seem to have been credited with a mostly antifungal function that ceases with the death of the plant. These are the

types of secondary metabolites most widely known to occur in the tribe Vernoniae, and the identity of the duct contents remains unresolved.

It seemed particularly useful to examine the corolla lobes of the two South American species that had thus far been retained in *Vernonia* on the basis of the pollen and habit of the plants. Their position in *Vernonia* was always in question because of their remote geographical locations in Argentina, Brazil, Paraguay and Uruguay. The material was chosen from herbarium specimens that showed no indication of being preserved in alcohol or formalin. As shown in the figures (1G, H) no trace of multiple longitudinal ducts was seen. The character of the ducts is here regarded as a defining feature of the generic group of *Vernonia*, *Vernonanthura* and *Trepadonia* and the lack of the feature in the two South American species, combined with the remote geographical location is considered strong evidence that they do not belong in *Vernonia*. DNA of the two species has not yet been sequenced, and their proper disposition remains to be determined.

Acknowledgements

Alice Tangerini of the Dept. of Botany is thanked for assembling the plate of illustrations.

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Appendix

Specimens used in microscopic illustrations

- Vernonanthura brasiliiana* (L.) H. Rob., Venezuela: Lara: vicinity of Barquisimeto, 4 Jan 1923, José Saer 102 (US).
- Vernonia angustifolia* Michx., Arlington VA, corner of N. Calvert and 18th Sts, unvouchered garden plant: Aug. 2015, H. Robinson s.n.
- Vernonia echiioides* Less., Brazil: Paraná, São João, in paludosis, 21 Mar. 1910, P. Dusén 9370 (US).
- Vernonia incana* Less., Paraguay: Dept. Neembucu, Dist. Yataity, Esterito, Jan 1975, M.A. Walter 118 (US).
- Vernonia noveboracensis* (L.) Michx., Washington, D.C., Roosevelt Island: 19 Aug. 2014, H. Robinson 14-1 (US).

Marrubium eriocephalum (Lamiaceae); a species new to the flora of Turkey, with contributions to its taxonomy

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Academic editor: Alan Paton | Received 10 August 2015 | Accepted 24 November 2015 | Published 12 January 2016

Citation: Firat M (2016) *Marrubium eriocephalum* (Lamiaceae); a species new to the flora of Turkey, with contributions to its taxonomy. *PhytoKeys* 58: 9–20. doi: 10.3897/phytokeys.58.5890

Abstract

Marrubium eriocephalum (Lamiaceae) is described as a new record for the Flora of Turkey (B9 Van). A detailed morphological description, photographs, distribution map, and pollen and nutlet morphology of this new record are given.

Keywords

New record, *Marrubium eriocephalum*, Van, Turkey

Introduction

The genus *Marrubium* L. includes annual and perennial herbs. Although species of this genus are mainly distributed in the Irano-Turanian and Mediterranean phytogeographic regions, some members are naturalized in Australia and America. The genus comprises about 40 taxa (Akgül et al. 2008). In Turkey, the genus is represented by 21 taxa, of which 12 are endemic to Turkey (Cullen 1982, Davis et al. 1988, Ekim et al. 2000, Aytaç et al. 2012). This endemism rate (57%) shows that Turkey is an important centre of diversity for the genus. Bentham (1834, 1848) first revised the genus and divided it into sections *Lagopsis* and *Marrubium*. Later, many who studied the genus divided it into several sections (Briquet 1986, Boisser 1879, Seybold 1978); however, in Turkey, *Marrubium* was not divided into sections in recent treatments by Cullen (1982) and Akgül (2004).

Pollen grain features are taxonomically significant. A large number of studies on pollen morphology in Lamiaceae can be found in the literature (Erdtman 1945, Celenk et al. 2008, Moon et al. 2008a, 2008b, 2008c, Hassan et al. 2009, Aytac et al. 2012). The seed surfaces of Lamiaceae have been studied by many researchers (Husain et al. 1990; Demissew and Harley 1992, Marin et al. 1996, Budantsev and Lobova 1997, Jamzad et al. 2000, Kaya et al. 2009, Kahraman et al. 2009, 2010, Akgül et al. 2008). In Lamiaceae pollen grains are reticulate, tricolpate or hexacolpate. (Erdtman 1945).

Erdtman (1945) studied *Marrubium* pollen grains. Abu-Asab and Cantino (1994) studied the pollen grains of Lamiaceae species, including the Turkish *Marrubium*. *Marrubium* pollen grains are tricolpate, radially symmetric and isopolar, and are prolate spheroidal and oblate spheroidal in shape (Erdtman 1969). There is no operculum. The aperture membranes are generally psilate or rarely granulate. The exine is tectate.

A detailed pollen morphological study of Turkish *Marrubium* species was undertaken by Akgül et al. (2008), where the pollen features of 19 Turkish taxa were examined and the pollen grains were divided into 3 groups: 1) the exine is psilate-perforate, psilate-foveolate and the pollen shape is prolate spheroidal, oblate-spheroidal; 2) the exine is granulate-perforate; and 3) the exine is reticulate, rugulate-reticulate and the pollen shape is prolate-spheroidal.

Lamiaceae nutlet surfaces are also taxonomically significant; they have different sizes and colours, so the nutlet morphology is used not only between the genera but also between subsections and subspecies (Husain et al. 1990). *Marrubium* nutlet surface morphology also has a systematic significance (Brochmann 1992, Hedge 1992).

Materials and methods

Marrubium eriocephalum Seybold, was collected in İspiriz Mountains (Fig. 1), Van in October 2013–2014. Cullen (1982), and Güner (2000) did not record this species in Turkey. Thus this collection constitutes a new record for the Turkey flora: Cullen (1982), Boissier (1859), Huber-Morath (1978), Seybold (1978), Özhatay et al. (2009), Özhatay and Kültür (2011), Akgül (2012) only recording *Marrubium eriocephalum* from South Kurdistan region of Iraq. Collected materials were deposited at the Herbarium of Yüzüncü Yıl University Science Faculty (VANF).

Marrubium eriocephalum pollen grains were studied using LM and SEM. The voucher specimens are listed in (Table 1). For the LM, the pollen grains were first treated with 70% alcohol and allowed to evaporate, and then embedded in glycerine jelly (Wodehouse 1935). The polar axis (P), equatorial axis (E), colpus length (Clt), colpus width (Clw), exine thickness (Ex), intine thickness (I), and apocolpium diameter (Ap) were measured from at least 30 fully developed grains per sample under an Olympus BX21 microscope (1000×). For the SEM analyses, pollen grains obtained from each specimen were transferred onto stubs and coated with gold (JEOL JSM 7001-F). The methods of Henderson et al. (1968), Faegri and Iversen (1989), and Punt et al. (2007) were those mainly followed.

The seed morphology of this new record, *Marrubium eriocephalum*, was studied using SEM according to the methods of Murley (1951) and Koul et al. (2000).

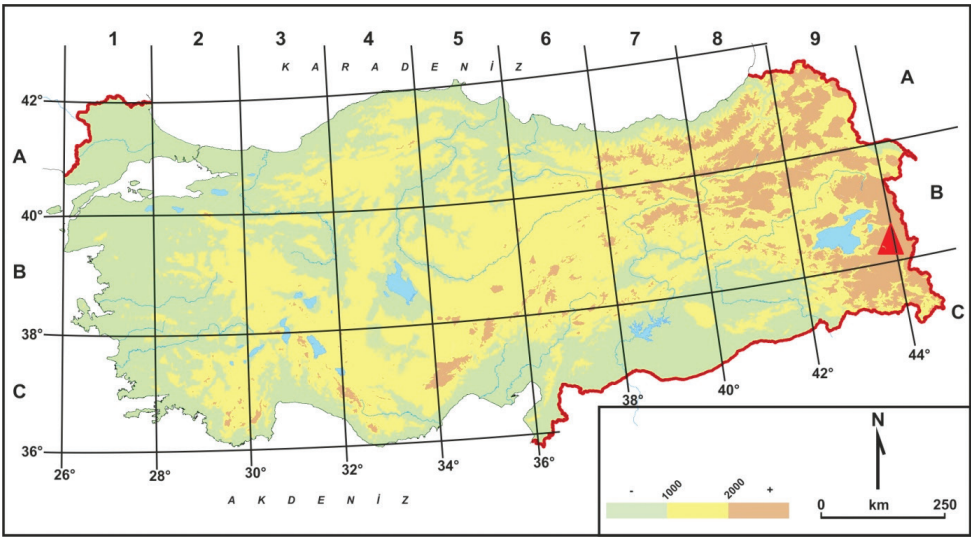


Figure 1. Geographical distribution of *Marrubium eriocephalum* Marooft (▲) in Turkey.

Table 1. Pollen morphology of *Marrubium eriocephalum* Unit is μm .

Taxon	Polar axis (μm)			Equatorial axis (μm)			P/E ratio	Exine (μm)	Intine (μm)	Ornamentation
	min	max	ort.	min	Max	ort	Shape			
<i>Marrubium eriocephalum</i>	24.96	31.20	27.49	29.12	33.28	30.75	0.89 oblate-spheroidal	1.91	1.14	Psilate-reticulate

Description

Marrubium eriocephalum

Type. Iraq: Perrish, 3340 m, 27.08.1957, Ali-al-Rawi & Serhang 24522, (holotypus K; <http://specimens.kew.org/herbarium/K000249641>). (Figs 2–3, Table 2).

Ascending erect, branched, perennial herb. Stems 15–50 cm, yellowish to greyish, densely white lanate hairy. Basal leaves elliptic to rotund, petiolate, petiole 8–20 mm, lamina 10–22×21–35 mm, irregularly or regularly crenate to serrate, densely lanate with stellate hairs. Cauline leaves petiolate, flabellate, lunate or rotund, irregularly or regularly crenate-serrate, and densely lanate with stellate hairs. Verticillasters, 1–3(5), globular 18–27 mm diameter, 15–35 flowered. Bracteoles subulate, as long as long calyx teeth, densely spreading stellate villous to lanate hairy, 10–14 mm. Calyx purplish to greenish, tubular, tube 5–7.5 mm long, 5 -toothed with teeth subequal 2.5–5.5 mm long, erect, long stellate hairy with short or sessile glandular hairs. Corolla yellowish sometimes purplish on upper lip, yellowish within lip, 7–11 mm long, 2-lipped; upper lip straight, bifid 0.5–1 mm long; lower lip 3-lobed, middle lobe of the lower lip 3–4 mm wide, densely long stellate hairy, lower part of the corolla tube sometimes with glabrous and/or a few sessile glandular hairy. Nutlets brownish to greenish, oblong,

Table 2. A comparison of selected morphological characters of *Marrubium eriocephalum* between descriptions given in the Type specimen and in the present study, *M. vanense* and *M. astracanicum*.

Morphological characters	<i>M. eriocephalum</i> (Type specimen)	<i>M. eriocephalum</i> (The findings of present study)	<i>M. vanense</i>	<i>M. astracanicum</i>
Stems	suffrutescent, multi stemmed, 15–25 cm long	ascending erect, branched, 15–50 cm long	erect, 50 cm or more	erect, somewhat branched, (15-)25–50(-70) cm
Indumentum	densely white velutinous hairy	yellowish to greyish, densely white lanate hairy	longer and shorter simple hair	densely stellate-pilose, glabrescent
Basal leaves	rotund, cuneata, irregular crenate, up to 20×20 mm	elliptic to rotund, irregularly or regularly crenate to serrate, lamina 10–22×21–35 mm	elliptic to ovate, crenate	elliptic-obovate, crenate
Cauline leaves	leaves rounded	petiolate, flabellat, lunat-rotund, irregularly or regularly crenate-serrate	Petiolate, ± orbicular or flabellate, irregularly and coarsely crenate	long-petiolate, orbicular to elliptic-obovate, deeply and irregularly crenate-serrate
Leaves petiol	up to 15 mm long	8–20 mm long	15–30 mm long	5–15 mm long
Verticillasters	23–25 mm diameter, 20–30 flowers	18–27 mm diameter, 15–35 flowers	15–25 mm diameter, 15–25 flowers	10–15 mm, 15–20 flowers
Bracteoles	subulate, 8–10 mm long, distinctly hairy with long white pilose	subulate, 10–14 mm long as long as long calyx teeth, densely spreading stellate villous to lanate hairy	subulate, 4–5 mm long, as long as calyx tube	Subulate, 5.5–9 mm long, as long as calyx teeth
Calyx	calyx tube 4.5 mm, densely white glandular pilose hairy, purple; calyx teeth 5, straight or spreading, purple, 2.5 mm long, subequal, apical pilose hairy	calyx tube 5–7.5 mm purplish to greenish, tubular, 5 subequal teeth and teeth 2.5–5.5 mm long, erect, long stellate hairy with short or sessile glandular hairs	Calyx tube 4.5–5 mm, with stellate hairs; teeth 5 or rarely 6, somewhat unequal, 2.5 mm, straight, erect or slightly spreading, covered with stellate hairs for 1/2-2/3 of their length	Calyx tube 4-5 mm, sparsely to densely spreading pilose with stellate hairs with elongate central branches. Teeth 1-4 mm, usually dark purple, straight, erect, stellate-pilose for c. 2/3 of their length
Corolla	purple, 6–8 mm, galea 1.5 mm, third part bifid, galea 3–4 mm with lip	yellowish sometimes purplish on upper lip, yellowish within lip, 7–11 mm long, upper lip (galea) 0.5–1 mm, 2-lipped; upper lip straight, bifid; lower lip 3-lobed, middle lobe of the lower lip 3–4 mm wide, densely long stellate hairy, lower part of the corolla tube sometimes with glabrous and/or a few sessile glandular hairy	yellowish-white, densely lanate with stellate hairs outside, upper lip glabrous inside	lavender, mauve or purple, 10-14 mm, densely stellate pubescent outside, ±glabrous within upper lip.
Nutlets	unknown	brownish to greenish, oblong, 2.5–3.4 mm long×1.1–2.1 mm wide.	oblong, brown-dark brown, 2 mm long×1.3 mm wide.	oblong, brown, 1.9 mm long×1.1 mm wide.

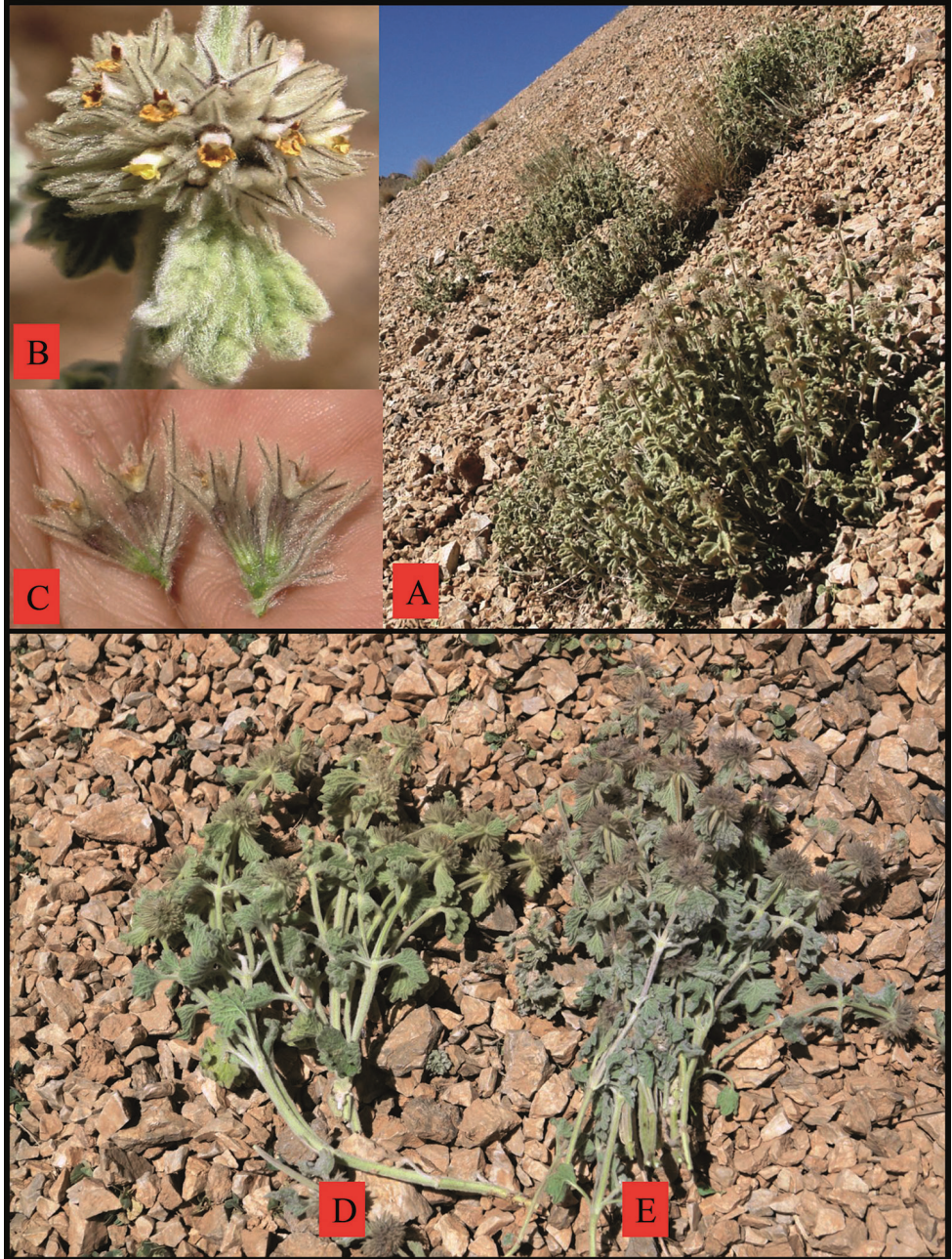


Figure 2. *Marrubium eriocephalum* **A** habit and habitat **B** flowers **C** calyx and bracteoles **D** yellowish form **E** greyish form.

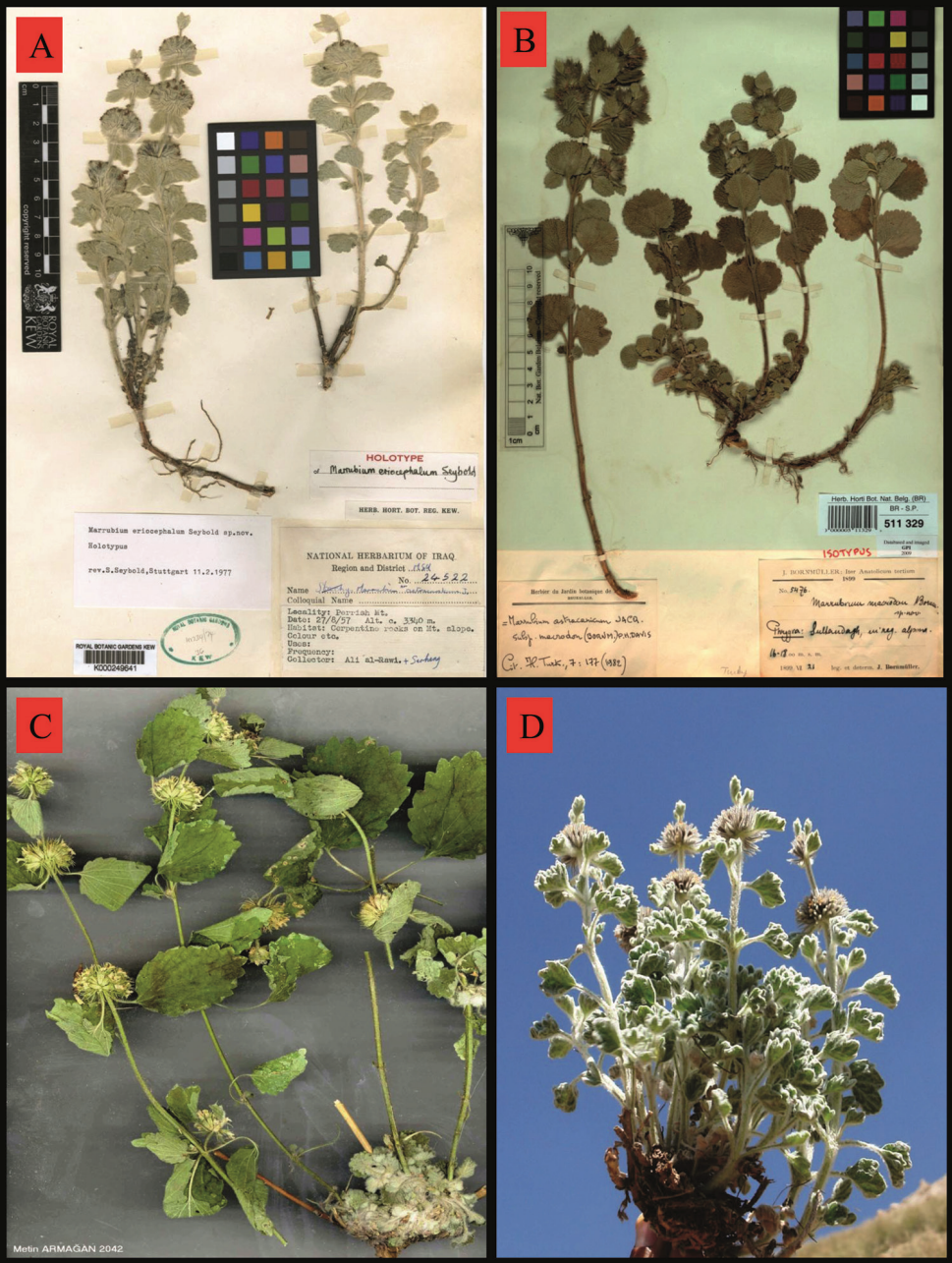


Figure 3. **A** *Marrubium eriocephalum* holotype Ali-al-Rawi&Serhang 24522 K **B** *Marrubium astracanicum* Isotype Bornmueller 5476 K **C** *Marrubium vanense* Metin Armağan 2042 VANF **D** *Marrubium eriocephalum* habit (İspiriz Mountains-fresh).

2.5–3.4 × 1.1–2.10 mm, verrucate. Pollen grains isopolar, tricolpate, oblate (P/E 0.89), polar axis (P) 27.49 µm, equatorial axis (E) 30.75 µm, amb triangular, exine 1.91 µm, the colpus membrane granulate, exine psilate- reticulate.

Examined material. Turkey. B9 Van; Başkale, İspiriz Mountains West, Serpentine rocks, 3259 m, 38°04'17"N, 43°56'23"E, 11.09.2013, *M. Fırat* 30289 & E. *Hamzaoğlu* (in flower), VANF; ibid *M. Fırat* 30335 (in fruit) VANF; B9 Van; Başkale, İspiriz Mountains East, Mobile limestone screes, near serpentine rocks, 3419 m, 38°05'04"N, 43°57'26"E, 15.09.2014, *M. Fırat* 31010 (in flower), VANF.

Habitat. Mobile limestone screes, near serpentine rocks, 3200–3500 m, in very sparse vegetation.

Phenology. Flowering and fruiting times from August–October.

Distribution in Turkey. Van province.

General distribution. Kurdistan region of Iraq, Turkey.

Associated with. *Allium oreophilum* C.A.Mey., *Didymorphysa aucheri* Boiss., *Jurinea moschus* (Hablitz) Bobrov subsp. *moschus*, *Heracleum* sp.

Vernacular name. In Van province, indigenous people use the name “Bizbizok” for *Marrubium* (Fırat 2013).

Results

Palynological investigation

The pollen grains were measured and photos were taken with an Olympus BX21 light microscope. The pollen type, exin surface ornamentation, and SEM microphotography were recorded. The seed sizes were measured and the surface ornamentation was scrutinized with SEM microphotography.

The *Marrubium* pollen grain measurements are given in (Table 1). The pollen grains were isopolar, tricolpate, and oblate (P/E 0.89), with a polar axis (P) of 27.49 µm and an equatorial axis (E) of 30.75 µm. The amb was triangular, the exine was 1.91 µm thick, the colpus membrane was granulate, and the exine was psilate- reticulate (Table 1, Fig. 4)

Nutlet morphology

The nutlet morphology of *Marrubium eriocephalum* was studied herein for the first time. Nutlet of the species were large, brown, and elliptic. The average nutlet size was 2.5–3.48 × 1.18–2.10 mm. There were polygonal cells in the nutlet epicarp and the ornamentation was verrucate.

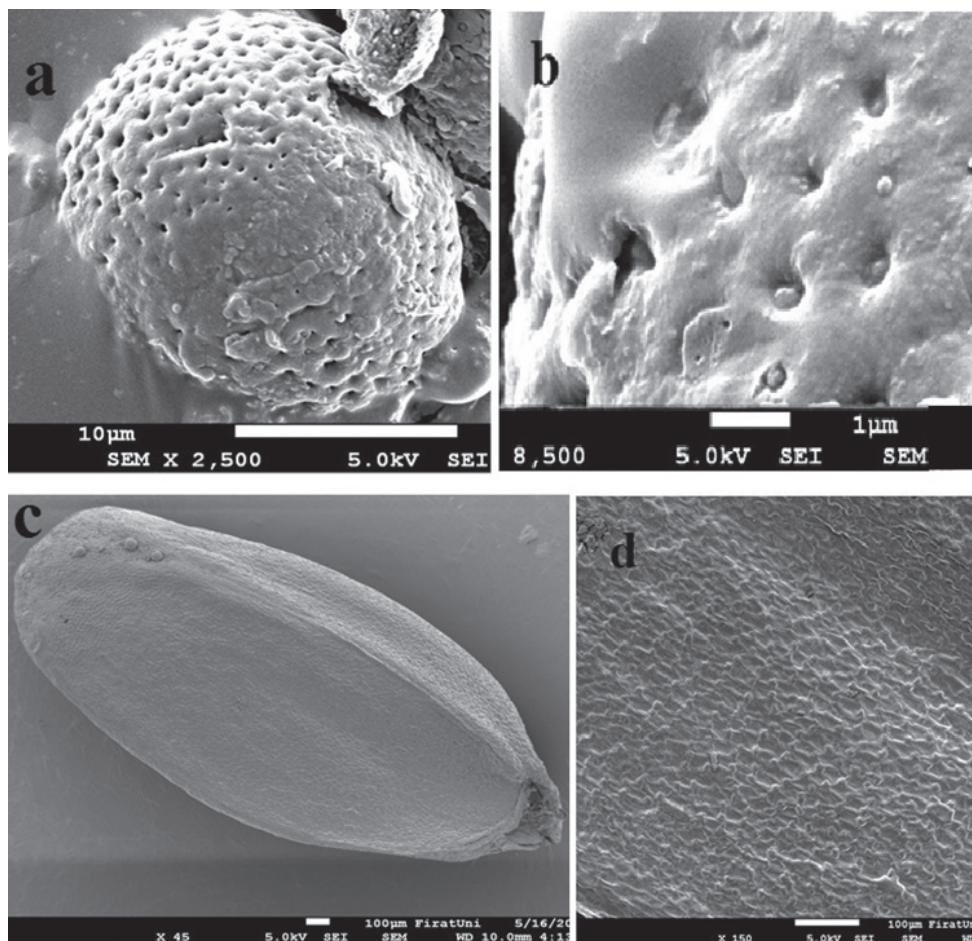


Figure 4. SEM photos of the pollen grains and seed coat of *Marrubium eriocephalum*; **a** equatorial view ($\times 2500$) **b** detail of pollen grains ($\times 8500$) **c** general shape of seed coat ($\times 45$) **d** seed coat surface ($\times 150$).

Discussion

The *Marrubium eriocephalum* was first collected from the Kurdistan region of Iraq by Ali-al-Rawi & Serhang, and described as a new species by Seybold (1978). Differences based on observations and measurements during 2-year field trips and herbarium studies, between type specimens and our material, are shown in Table 2. Specifically, Seybold described the species as having purple flowers; however, our findings showed that the species has yellowish flowers with purple upper lips. We believe that this error was due to the fact that the observations by Seybold were based solely on herbarium material. However, the author of *Marrubium eriocephalum*, Seybold (1978) claimed that *Marrubium astracanicum* is a species close to *Marrubium eriocephalum*, yet our findings showed that *Marrubium vanense* Hub.-Mor. is closer to *Marrubium eriocephalum* according to Flora of Turkey (Table 1, Fig. 3) in stem height, bracteole length and leaf indumentum.

Our palynological findings were compared with those of the study of Akgül et al. (2008) and according to their classification, *Marrubium eriocephalum* is classified as the third type. Due to its oblate-spheroidal pollen grains, psilate-reticulate ornamentation, and tricolpate aperture, our pollen showed similarities with *Marrubium vanense* and *Marrubium catariifolium* Desr. However, *Marrubium catariifolium* is different from *M. eriocephalum* in being an annual, with white flowers in 5-8 flowered verticillasters Cullen (1982).

In Flora of Turkey, the nutlet features of *Marrubium vanense* and *Marrubium catariifolium* are described. Both species have oblong, brown-dark brown nutlet with verrucate ornamentation. Our investigation showed similarities with the nutlet features of *Marrubium vanense*, *Marrubium catariifolium*, and *Marrubium eriocephalum*, which are oblong, brown, and verrucate in ornamentation.

Key to closely related *Marrubium* species in Turkey

- 1 Corolla mauve to purple *M. astracanicum*
- Corolla white, cream or yellowish, rarely pinksh 2
- 2 Verticillasters 1-flowered, disposed in long ‘spikes’ *M. depauperatum*
- Verticillasters several-flowered, not disposed in ‘spikes’ 3
- 3 Plants widely and divaricately branched; calyx teeth stellate- pubescent to apex *M. peregrinum*
- Plants unbranched, or with few, erect branches; calyx teeth usually with upper 1/3 or 1/2 glabrous. 4
- 4 Stems 50 cm or more; calyx tube greenish; leaves with simple hairs above *M. vanense*
- Stems 50 cm or less; calyx tube purplish to greenish; leaves with densely stellate lanate above..... *M. eriocephalum*

Acknowledgements

Thanks to Dr. Birol Başer for pollen studies in the manuscript, to Dr. Ferhat Celep for support new description about the manuscript and special thanks Kurtuluş Özgişi for check English grammar.

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Floristic survey of herbaceous and subshrubby aquatic and palustrine angiosperms of Viruá National Park, Roraima, Brazil

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Academic editor: *R.P. Oliveira* | Received 29 April 2015 | Accepted 18 November 2015 | Published 12 January 2016

Citation: Costa SM, Barbosa TDM, Bittrich V, Amaral MCE (2016) Floristic survey of herbaceous and subshrubby aquatic and palustrine angiosperms of Viruá National Park, Roraima, Brazil. *PhytoKeys* 58: 21–48. doi: 10.3897/phytokeys.58.5178

Abstract

We provide and discuss a floristic survey of herbaceous and subshrubby aquatic and palustrine angiosperms of Viruá National Park (VNP). The VNP is located in the northern Amazon basin and displays phytophysiognomies distributed in a mosaic where these plants occur, as flooded forests, hydromorphic white-sand savannas, “*buritizais*” and waterbodies. After expeditions between February/2010 and January/2015 and the analysis of specimens from regional herbaria, we list 207 species of herbaceous and subshrubby aquatic and palustrine angiosperms for the VNP, distributed in 85 genera in 37 families. We recorded six new occurrences for Brazil, two for the northern Brazilian region and 21 for Roraima state. These new occurrences, added to the other species listed here, highlight the floristic similarity between the study site and the Guiana Shield, an adjacent phytogeographical unit and geologically related to the origin of white-sand savannas.

Resumo

(Lista Florística de angiospermas herbáceas e subarborescentes aquáticas e palustres do Parque Nacional do Viruá, Roraima, Brasil) Esse estudo foi realizado objetivando a elaboração de uma lista florística das angiospermas herbáceas e subarborescentes aquáticas e palustres do Parque Nacional do Viruá (PNV). O PNV está localizado na região norte da Bacia Amazônica e apresenta fitofisionomias distribuídas em mosaico onde esse grupo de plantas ocorre, como florestas inundáveis, savanas sobre solos de areia branca hidromórficas,

buritizais e corpos d'água. Após coletas entre Fevereiro/2010 e Janeiro/2015 e a análise de espécimes depositados em herbários regionais, foram listadas 207 espécies de angiospermas herbáceas e subarborescentes aquáticas e palustres no PNV, distribuídas em 85 gêneros e 37 famílias. Foram registradas seis novas ocorrências para o Brasil, duas para a região norte do Brasil e 21 para o estado de Roraima. Essas novas ocorrências, juntamente com as demais espécies listadas, evidenciam a similaridade florística entre a área de estudo e o Escudo das Guianas, uma unidade fitogeográfica adjacente e geologicamente relacionada com a origem das savanas sobre solos de areia branca.

Keywords

“Campinaranas”, Guiana Shield, flora, aquatic macrophytes

Palavras-chave

“Campinaranas”, Escudo das Guianas, flora, macrófitas aquáticas

Introduction

Aquatic and palustrine (A&P) plants are able to survive in permanent or periodic submersion of at least their root system and share a few of the adaptations to these habitats (Sculthorpe 1967, Philbrick and Les 1996, Amaral et al. 2008). These plants form an artificial group that includes bryophytes, ferns and angiosperms (Sculthorpe 1967, Chambers et al. 2008) and contains species with pronounced phenotypic plasticity (Sculthorpe 1967) which hinder their identification. The use of several bibliographic resources and the detailed examination of specimens are indispensable for a reasonably reliable identification. Concurrently, there are a number of difficulties and peculiarities related to the collecting and preservation process (Fidalgo and Bononi 1989) such as the need of boats, recipients and special papers to press the plants correctly.

Aquatic and palustrine species are important for the structure and maintenance of the habitats where they occur. These plants determine the environmental heterogeneity and water quality of natural and artificial waterbodies (Junk 1986, Cronk and Fennessy 2001). Studies on A&P plants in the Neotropics focus mainly on ecological analyses, while floristic and taxonomic analyses are sparse (Padial et al. 2008, Piedade et al. 2010).

The Amazon region contains complex river systems with different physicochemical characteristics resulting in two contrasting types of inundated forests, one known as *várzea* – along white-waters rivers rich in nutrients and suspended sediment – and the other as *igapó* – along rivers poor in nutrients and, generally, poor in suspended sediments with dark or clear waters (Pires and Prance 1985). These distinctions arise from the origin and drainage areas of rainwater and directly influence the diversity of plants, particularly A&P ones. According to Piedade et al. (2010), studies focusing on the richness and ecology of wetland plants are more common in areas of *várzea* and inventories are still needed in *igapó* areas.

The Viruá National Park (VNP) is among the few protected areas that preserves ecosystems favorable to wetland communities. It receives water discharges from differ-

ent rivers, of different sizes and mostly with *igapó* characteristics (Junk et al. 2011). The distribution of the vegetation in the VNP shows a mosaic-like organization with large areas where the soil is permanently or periodically submersed or saturated with water (mainly white-sand savannas, locally known as “*campinaranas*”) (ICMBio 2014). The white-sand savannas can vary from a forested to herbaceous physiognomy (Velooso et al. 1991); this gradual change may be associated with the increasing waterlogging of the soils (Mendonça 2011). The herbaceous physiognomy of white-sand savannas covers about 25% of the VNP (ICMBio 2014).

Reports of some preliminary studies in the VNP mention a high floristic richness (Gribel et al., unpublished data) but unfortunately, if there are vouchers from these expeditions, none are in any herbaria known to us. Additionally, Gribel et al. (unpublished data) rarely identified herbs and subshrubs at species level, and often listed wetland plants by popular names or only at family or genus level. In fact, these authors never published formal checklists or indicated the material identified during their inventories.

Keeping in mind the existence of vast areas of periodically or permanently inundated ecosystems in the Viruá National Park and the lack of knowledge relative to wetland plants in the region and in areas influenced by *igapó* rivers, we provide and discuss the floristic survey of herbaceous and subshrubby aquatic and palustrine angiosperms found there.

Methods

Study area

The Viruá National Park (VNP; Figure 1) is located in the Caracaraí district, Roraima state, northern Brazil (1°19'11"N; 61°7'17"W DMS). The climate in the region is equatorial with the rainy season intercalated by a more or less short dry season, between October and March (ICMBio 2014). This protected area presents igneous volcanic or metamorphic rocks in the hills and sandy soil of fluvial, aeolian or weathering sedimentary origin in the plains (ICMBio 2014).

The VNP contains in its 227,011 ha different plant formations distributed in a mosaic (ICMBio 2014) (Figures 1–2): rainforest – typical forested formation of amazon region; white-sand savannas- sandy and leached, forested to grassy, hydromorphic or non-hydromorphic plain areas; and “buritizais” – flooded areas dominated by *Mauritia* palms. The protected area has its western boundary at the Branco River, a line drawn a few kilometers from an abandoned fragment of the BR-174 road (known as “Estrada Perdida”) as the northern and the eastern boundaries, and by the Anauá River in the southern limit. In addition to the water discharges received from rivers mentioned above, it also receives water from the Barauana River, situated to the east and beyond the limits of the VNP, from the Iruá River, in a south-north axis, and a dense network of streams within its boundaries (ICMBio 2014).

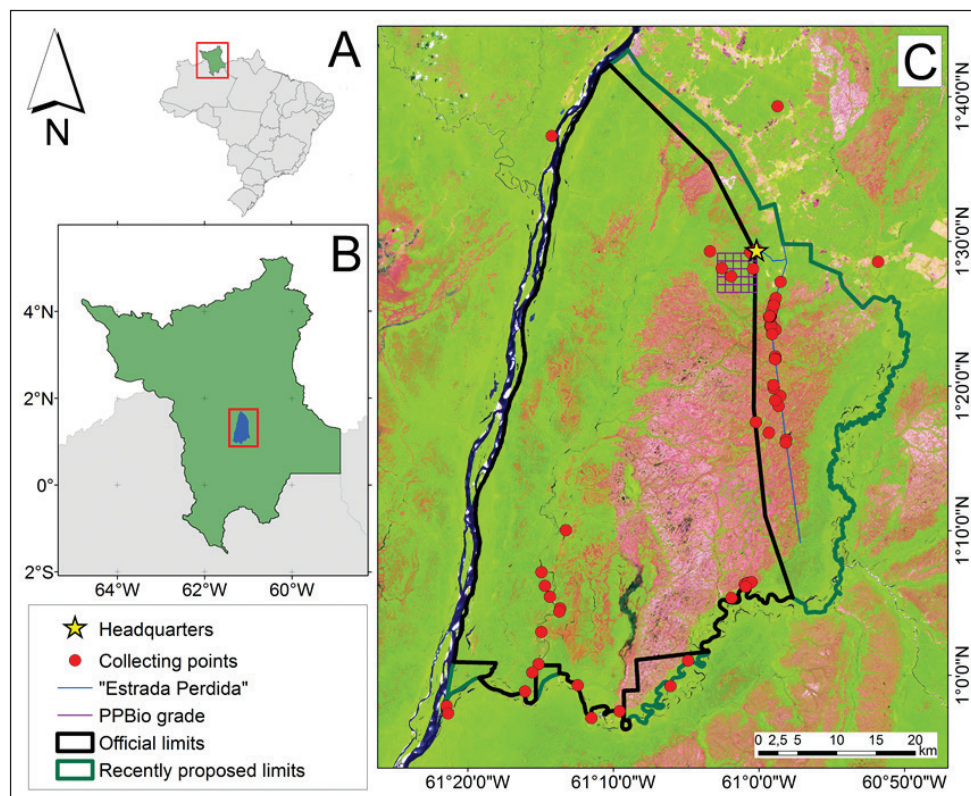


Figure 1. Viruá National Park (location). **A** Roraima state in Brazil **B** the VNP in the central-southern region of Roraima **C** the actual limits of protected area (black line), the area aimed to be included during extension (green line) and the collecting points [.shp files provided by IBGE and the VNP administration]

Collecting and analyzing data

We investigate the herbaceous and subshrubby aquatic and palustrine angiosperms. The expeditions to collect fertile botanical samples encompassed the local dry and wet seasons, between February/2010 and January/2015. We followed Fidalgo and Bononi (1989) for both the collecting and the herborization processes and vouchers are deposited mainly at INPA and UEC herbaria. When available, we sent duplicates to UFP and/or UFRR herbaria. The acronyms are according to Index Herbariorum (Thiers 2015, continuously updated). Our inventory also included specimens previously collected in the study area and deposited at INPA, MIRR and UFRR herbaria.

We chose the collecting points non-systematically but they tended to be more concentrated in peripheral areas and along “Estrada Perdida”, due to their accessibility, and in areas where aquatic and palustrine plants are abundant (white-sand savannas of hydromorphic soils, “buritizais” and waterbodies) (Figure 1). Even though the “Estrada Perdida” is outside of the current protected area, a proposal suggests the enlargement of VNP’s borders aiming for the inclusion of areas eastwards up to the margins

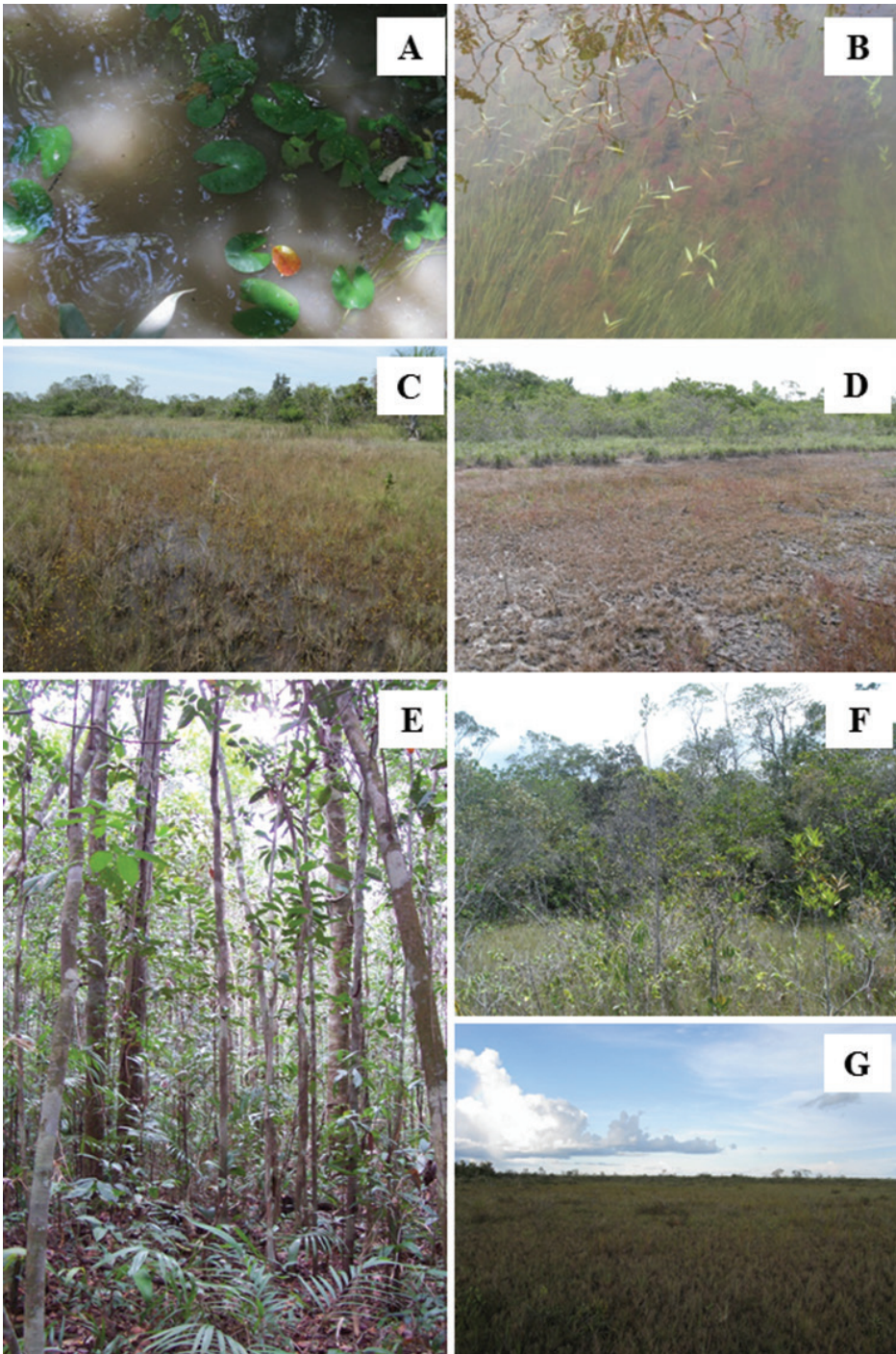


Figure 2. Viruá National Park: habitats and physiognomies. **A–B** waterbodies with turbid (**A**) and trans-lucid (**B**) water; **C–D** Areas with saturated soils during rainy season (**C**) and dry season (**D**); **E–G** Forested (**E** given by K.G. Cangani), arboreal (**F**) and herbaceous (**G**) white-sand savannas (“campinaranas”).

of the Barauana River, such that the “Estrada Perdida” would be enclosed in the VNP (ICMBio 2014).

Our identifications were based on regional floras of the Amazon and Guiana regions and specialized bibliography of each family: Core 1936, Organization for Flora Neotropica 1967-, Cook 1985, Cook and Urmi-König 1985, Kral 1988, 1992, Taylor 1989, 1991, Thomas 1992, 1997, Steyermark et al. 1995 – 2005, Araújo and Longhi-Wagner 1996, Camelbeke et al. 1997, Luceño et al. 1997, Kral and Jansen-Jacobs 1998, Wanderley et al. 2001-, Prata 2002, Gil and Bove 2004, Campbell 2005, Trevisan 2005, Simpson 2006, Thomas 2006, Rivadavia et al. 2009, Souza and Giulietti 2009, Wanderley 2011, Christenhusz 2014.

Additionally, we studied images of specimens deposited at F, K, MO, NY, P, and other herbaria with online digital images. We took into account the reliability of the identifications, with preference to types, historical collections and specimens identified by specialists; when available in the literature, we queried the original descriptions and revisions of genera or entire families. Moreover, we consulted specialists when necessary.

Rivadavia et al. (2009) described *Drosera amazonica* Rivadavia, A. Fleischm. & Vicent. and cited the VNP among the localities of its occurrence, and although we did not collect this species, it appears in our list. Pessoa et al. (2015) and Mota et al. (2015), respectively, held two taxonomic treatments with focus on Orchidaceae and Xyridaceae to this area, and we also included the aquatic and palustrine herbs and subshrubs cited by them in our list. When it was impossible to examine directly any specimen of the species treated, we cited the correspondent treatment.

Information on geographic distribution and authors of the species were based on TROPICOS (last access sept/2012), “Lista de Espécies da Flora do Brasil” (Forzza et al. 2015) and specialized literature for each family.

We classified the species analyzed according to morphoanatomical characters and indicated the functional ecological group that they belong (“life forms”). The categories represent a continuum from less to more specialized adaptations to the aquatic environment: palustrine plants (growing in saturated soils); emergent plants; rooted with floating leaves; free floating; and submersed plants (with life cycle entirely or partially under water) (Cronk and Fenessy 2001, Chambers et al. 2008).

For floristic comparisons, we unite some representative lists from northern Brazil and other adjacent floras, namely: savannas from northern Roraima (Miranda and Absy 1997), *Várzea* and *Igapó* areas (Piedade et al. 2010, Lopes et al. 2014; Junk and Piedade 1993, Conserva et al. 2008), Guiana Shield (Funk et al. 2007), and Northern Brazil (Moura-Júnior et al. 2015). We made an overall comparison between the lists and no richness or diversity index was estimated (Table 1).

Results

The INPA herbarium was the only that held older specimens collected in the study area. Our final list includes 207 species of A&P herbs and subshrubs, distributed in 85

Table 1. Aquatic and palustrine herbaceous and subshrubby angiosperms of the Viruá National Park [in brackets the number of genera and species of each family; (*) = new occurrences for Roraima state; (#) = new occurrences for northern Brazil; (&) = new occurrences for Brazil; (¥) = commercialization incompatible with species survival according to UNEP World Conservation Monitoring Centre; (\$) = in Brazil, occurs only in Roraima; pal = palustrine; emer = emergent; flouv = with floating leaves; float = free floating; sub = submerged. When the accepted names are different in the TROPICOS database and in Forzza et al. (2015), the name cited by the latter is listed in brackets; (*) = probably endemic to white-sand savannas; F=Funk et al. 2007; C = Conserva et al. 2008; P = Piedade et al. 2010, MJr = Moura Junior et al. 2015].

SPECIES	Life form	Occurrence in Brazil	Also listed at	Selected Vouchers
ALISMATACEAE (2/4)				
<i>Helanthium tenellum</i> (Martius) Britton	pal, emer, sub	???	F, MJr	TDM Barbosa 1094 (INPA, UEC)
<i>Sagittaria guayanensis</i> Kunth	emer, flouv	N, NE, CO, SE	M&A, F, MJr	TDM Barbosa 1097 (UEC)
<i>Sagittaria rhombifolia</i> Cham.	emer	N, NE, CO, SE, S	M&A, F, MJr	TDM Barbosa 1110 (INPA, UEC)
APOCYNACEAE (1/3)				
<i>Cynanchum guanchezii</i> Morillo	pal	N, NE	F	SM Costa 836 (INPA, UEC)
<i>Cynanchum sobradoi</i> Morillo [= <i>Ditassa sobradoi</i> (Morillo) Liedt]	pal	N	F	SM Costa 865 (UEC); TDM Barbosa 1241 (INPA)
<i>Cynanchum strictum</i> (Gleason & Moldenke) R.W.Holm * [= <i>Tasadia stricta</i> (E.Fourn.) Liedt & Rapini]	pal	N	F	SM Costa 994 (INPA, UEC)
ARACEAE (2/2)				
<i>Monnrichardia arborescens</i> (L.) Schott	pal, emer	N, NE, CO, SE	M&A, J&P, C, F, MJr	TDM Barbosa 768 (INPA, UEC)
<i>Pistia stratiotes</i> L.	float	N, NE, CO, SE, S	J&P, C, F, MJr	TDM Barbosa 1403 (UEC)
ARECACEAE (1/1)				
<i>Bactris campestris</i> Poepp.	pal	N, NE	F	MJG Hopkins 2181 (INPA), SM Costa 840 (UEC);
ASTERACEAE (1/1)				
<i>Eclipta</i> aff. <i>alba</i> (L.) Hassk.	pal	N, NE, CO, SE, S	J&P, F, MJr	SM Costa 968 (INPA, UEC)
BROMELIACEAE (1/1)				
<i>Ananas</i> cf. <i>parguazensis</i> Camarco & L.B.Sm.	pal	N	F	TDM Barbosa 1438 (INPA, UEC)
BURMANNIACEAE (1/2)				
<i>Burmamia bicolor</i> Mart.	pal	N, NE, CO, SE, S	F	SM Costa 870 (UEC), R Goldenberg 1606 (INPA)
<i>Burmamia capitata</i> (Walter ex J.F.Gmel.) Mart.	pal	N, NE, CO, SE, S	F	SM Costa 792 (INPA, UEC)

SPECIES	Life form	Occurrence in Brazil	Also listed at	Selected Vouchers
CABOMBACEAE (1/2)				
<i>Cabomba schwarzii</i> Rataj [= <i>Cabomba aquatica</i> Aubl.]	sub, fleav	N, NE, SE, S	F, P?, MJr?	TDM Barbosa 1230 (INPA, UEC)
<i>Cabomba furcata</i> Schult. & Schult. f.	sub, fleav	N, NE, CO, SE, S	F, MJr	TDM Barbosa 1201 (INPA, UEC)
CYPERACEAE (14-15/45)				
<i>Bulbosylis conifera</i> (Kunth) C.B. Clarke	pal	N, NE, CO, SE, S	M&A, F	TDM Barbosa 1392 (INPA, UEC)
<i>Bulbosylis junciformis</i> (Kunth) C.B. Clarke	pal	N, NE, CO, SE, S	M&A, F	TDM Barbosa 1115 (INPA, UEC)
<i>Bulbosylis lanata</i> (Kunth) Lindm.	pal	N, NE	M&A, F	TDM Barbosa 1331 (INPA, UEC)
<i>Calyptracarya monocephala</i> Hochst. ex Steud. ^s	pal	N	F	TDM Barbosa 1294 (INPA, UEC)
<i>Cyperus aggregatus</i> (Willd.) Endl.	pal	N, NE, CO, SE, S	M&A, F, MJr	TDM Barbosa 1113 (INPA, UEC)
<i>Cyperus haspan</i> L.	pal, emer	N, NE, CO, SE, S	M&A, J&P, F, MJr	TDM Barbosa 1104 (INPA, UEC)
<i>Cyperus simplex</i> Kunth	pal	N, NE, CO, SE	F	TDM Barbosa 1413 (INPA, UEC)
<i>Cyperus surinamensis</i> Rottb.	pal	N, NE, CO, SE, S	M&A, J&P, C, F, MJr	TDM Barbosa 1112 (INPA, UEC)
<i>Cyperus</i> sp.	pal	-		TDM Barbosa 1404 (INPA, UEC)
<i>Diplacrum</i> cf. <i>capitatum</i> (Willd.) Boeckler	pal, emer	N, NE, CO	F	TDM Barbosa 1126 (INPA, UEC)
<i>Diplacrum guianense</i> (Nees) T.Koyama	pal, emer	N, CO	F	SM Costa 924 (INPA)
<i>Eleocharis acutangula</i> (Roxb.) Schult.	pal, emer	N, NE, CO, SE, S	F	TDM Barbosa 1195 (UEC)
<i>Eleocharis fluctuans</i> (L.T. Eiten) E.H. Roalson & C.E. Hinchliff	sub	N	F	TDM Barbosa 1237 (INPA)
<i>Eleocharis geniculata</i> (L.) Roem. & Schult.	pal, emer	N, NE, CO, SE, S	C, F, MJr	EM Pessoa 790 (INPA)
<i>Eleocharis interstincta</i> (Vahl) Roem. & Schult.	pal, emer	N, NE, CO, SE, S	M&A, C, F, MJr	TDM Barbosa 1298 (INPA, UEC)
<i>Eleocharis</i> sp	sub	-		
<i>Exochogyne amazonica</i> C.B. Clarke	pal	N, NE, CO, SE	F	SM Costa 737 (INPA, UEC)
<i>Fimbristylis uhlhii</i> (Lam.) Link.	pal	N, NE	F	SM Costa 1005 (INPA)
<i>Fuirena umbellata</i> Rottb.	pal, emer	N, NE, CO, SE, S	M&A, C, F, MJr	TDM Barbosa 1253 (INPA, UEC)
<i>Hypochaeris pulchrum</i> (Rudge) H. Pfeiff.	pal	N, NE	F	TDM Barbosa 1164 (INPA, UEC)
<i>Lagenocarpus celiae</i> T. Koyama & Maguire ⁺	pal	N	F	TDM Barbosa 1263 (INPA, UEC)
<i>Lagenocarpus eriopodus</i> T.Koyama & Maguire ⁺⁺	pal, emer	N	F	SM Costa 1167
<i>Lagenocarpus glomerulatus</i> Gilly	pal	N	F	SM Costa 793 (INPA, UEC)
<i>Lagenocarpus rigidus</i> (Kunth) Nees	pal	N, NE, CO, SE, S	M&A, F	SM Costa 938 (INPA, UEC)

SPECIES	Life form	Occurrence in Brazil	Also listed at	Selected Vouchers
<i>Lagenocarpus sabanensis</i> Gilly	pal	N	F	FRC Costa 1650 (INPA)
<i>Lagenocarpus verticillatus</i> (Spreng.) T.Koyama & Maguire [= <i>Cryptangium verticillatum</i> (Spreng.) Vitor]	pal	N, NE, CO, SE	F	SM Costa 803 (INPA, UEC)
<i>Oxycaryum cubense</i> (Poepp. & Kunth) Lye	emer	N, NE, CO, SE, S	C, F, MJr	SM Costa 971 (INPA, UEC)
<i>Pycnus polystachyos</i> (Rortb.) PBeauv.	pal	N, NE, CO, SE, S	F, MJr	SM Costa 1004 (INPA), TDM Barbosa 1075 (UEC)
<i>Rhynchospora barbata</i> (Vahl) Kunth	pal	N, NE, CO, SE	M&A, F, MJr	TDM Barbosa 1328 (INPA, UEC)
<i>Rhynchospora cephalotes</i> (L.) Vahl	pal	N, NE, CO, SE	M&A, F	TDM Barbosa 1189 (INPA, UEC)
<i>Rhynchospora enaciata</i> (Nees) Boeck.	pal	N, NE, CO, SE, S	M&A, F, MJr	TDM Barbosa 1127 (INPA)
<i>Rhynchospora globosa</i> (Kunth) Roem. & Schult.	pal, emer	N, NE, CO, SE, S	M&A, F, MJr	SM Costa 988 (INPA, UEC)
<i>Rhynchospora hirsuta</i> (Vahl) Vahl	pal	N, NE, CO	M&A, F	SM Costa 733 (INPA, UEC)
<i>Rhynchospora holchoenoides</i> (Rich.) Herter	pal, emer	N, NE, CO, SE, S	M&A, F, MJr	TDM Barbosa 1076 (INPA, UEC)
<i>Rhynchospora longibnata</i> Boeck.	pal, emer	N	F	SM Costa 864 (INPA, UEC)
<i>Rhynchospora maguireana</i> T. Koyama ^{&}	pal, emer	-	F	TDM Barbosa 1169 (INPA, UEC)
<i>Rhynchospora riparia</i> (Nees) Boeck.	pal	N, NE, CO, SE, S	F	TDM Barbosa 1123 (INPA)
<i>Rhynchospora rugosa</i> (Vahl) Gale	pal	N, NE, CO, SE, S	F	TDM Barbosa 1278 (INPA, UEC)
<i>Rhynchospora schomburgkiana</i> (Boeck.) T. Koyama	pal	N	F, MJr	TDM Barbosa 1432 (INPA, UEC)
<i>Rhynchospora trichochaeta</i> C.B.Clarke *	pal	N, NE, CO	F	TDM Barbosa 1326 (INPA, UEC)
<i>Rhynchospora trispicata</i> (Nees) Schrad.	pal, emer	N, NE, CO	F	TDM Barbosa 1254 (INPA, UEC)
<i>Scleria amazonica</i> Camelbeke, M.Strong & Goergh. ^{&}	pal, emer	-	F	TDM Barbosa 1259 (INPA, UEC)
<i>Scleria cyperina</i> Kunth	pal	N, NE, CO, SE	F	SM Costa 890 (INPA, UEC)
<i>Scleria</i> cf. <i>lacustris</i> C.Wright	emer	N	F	TDM Barbosa 1267 (INPA, UEC)
<i>Scleria reticularis</i> Michx.	pal	N, NE		SM Costa 720 (INPA, UEC)
DROSERACEAE (1/2)				
<i>Drosera amazonica</i> Rivadavia, A. Fleischm. & Vicent.	pal	N (<i>vide</i> Rivadavia et al. 2009)	-	(<i>vide</i> Rivadavia et al. 2009)
<i>Drosera kaitetensis</i> Brumm.-Ding. ^{&}	pal		F	TDM Barbosa 1284 (INPA, UEC)
ERIOCAULACEAE (4/15)				
<i>Eriocaulon setaceum</i> L.	sub	N, CO, SE		TDM Barbosa 1219 (UEC)
<i>Eriocaulon tenuifolium</i> Klotzsch ex Körn. ^{&}	pal, emer, sub	N	F	TDM Barbosa 1051 (UEC)

SPECIES	Life form	Occurrence in Brazil	Also listed at	Selected Vouchers
<i>Paepalanthus tortilis</i> (Bong.) Mart.	pal	N, NE, SE	F	TDM Barbosa 1064
<i>Syngonanthus anomalus</i> (Körn.) Ruhland	sub	N	F, MJr	MCE Amaral 2011/17 (UEC)
<i>Syngonanthus caulescens</i> (Poit.) Ruhland	pal	N, NE, CO, SE, S	F, MJr	SM Costa 726 (UEC)
<i>Syngonanthus cuyabensis</i> (Bong.) Giul., Hensold & L.R. Parra*	pal	N, NE, CO, SE	F	FN Cabral 501 (UEC)
<i>Syngonanthus fenestratus</i> Hensold	pal	N	F	MCE Amaral 2011/26 (UEC)
<i>Syngonanthus gracilis</i> (Bong.) Ruhland	pal	N, NE, CO, SE, S	F, MJr	SM Costa 702 (UEC)
<i>Syngonanthus humboldtii</i> (Kunth) Ruhland	pal	N, NE, CO	F	TDM Barbosa 1046 (UEC)
<i>Syngonanthus longipes</i> Gleason	pal	N, CO	F	SM Costa 787 (UEC)
<i>Syngonanthus spongiosus</i> Hensold	pal	N		MCE Amaral 2011/5 (UEC)
<i>Syngonanthus tenuis</i> (Kunth) Ruhland	pal	N, CO	F	MCE Amaral 2011/29 (UEC), TDM Barbosa 1220 (INPA)
<i>Syngonanthus trichophyllus</i> Moldenke	pal	N	F	TDM Barbosa 1321 (UEC)
<i>Syngonanthus umbellatus</i> (Lam.) Ruhland	pal	N, CO, SE	F	SM Costa 736 (INPA, UEC)
<i>Tonina fluviatilis</i> Aubl.	pal	N, NE, SE	F, MJr	TDM Barbosa 1066 (INPA, UEC)
EUPHORBACEAE (1/1)				
<i>Croton suberratus</i> Jabl. &	emer	-		TDM Barbosa 1080 (UEC)
GENTIANACEAE (3/4)				
<i>Chelonanthus alatus</i> (Aubl.) Pulle	pal	N, CO	F	TDM Barbosa 1059 (INPA)
<i>Coutoubea reflexa</i> Benth.	pal	N	F	TDM Barbosa 1139 (INPA, UEC)
<i>Irishachia pratensis</i> (Kunth) L.Cobb & Maas *	pal, emer	N	F	SM Costa 932 (INPA, UEC)
<i>Irishachia pumila</i> (Benth.) Maguire *	pal	N	F	TDM Barbosa 1067 (UEC)
HAEMODORACEAE (1/1)				
<i>Schiokia orinocensis</i> (Kunth) Meisn.	pal	N, NE, CO	M&A, F, MJr	TDM Barbosa 1194 (UEC)
HYDROCHARITACEAE (1/1)				
<i>Elodea granatensis</i> Bonpl. [= <i>Apalanthe granatensis</i> (Bonpl.) Planch.]	sub	N, NE, CO, SE	F, MJr	TDM Barbosa 1323 (INPA)
LEGUMINOSAE (2/2)				
<i>Aeschynomene scabra</i> G.Don*	pal, emer	NE	F	MCE Amaral 2011/13 (UEC)
<i>Zornia latifolia</i> Sm.	pal	N, NE, CO, SE, S	F, MJr	TDM Barbosa 1118 (INPA, UEC)
LENTIBULARIACEAE (2/25)				
<i>Genlisea filiformis</i> A.St.- Hil.	pal	N, NE, CO, SE	F	SM Costa 715b (INPA, UEC)

SPECIES	Life form	Occurrence in Brazil	Also listed at	Selected Vouchers
<i>Genlisea oxycentron</i> A.St.-Hil.*	pal	N, NE		SM Costa 715a (INPA, UEC)
<i>Genlisea pygmaea</i> A.St.- Hil.	pal	N, NE, CO, SE	F	SM Costa 698 (INPA, UEC)
<i>Utricularia amethystina</i> Salzm. ex A. St.-Hil. & Girard	pal	N, NE, CO, SE	F	SM Costa 695 (INPA, UEC)
<i>Utricularia benjaminiana</i> Oliv. [§]	sub	N	F	TDM Barbosa 1106 (INPA, UEC)
<i>Utricularia breviscapa</i> Wright ex Griseb.	sub	N, NE, CO, SE	F, MJr	SM Costa 858 (INPA, UEC)
<i>Utricularia chiriquiensis</i> Fernandez-Pérez*	pal	N	F	SM Costa 779 (INPA, UEC)
<i>Utricularia costata</i> P. Taylor	pal	N, NE, CO	F	TDM Barbosa 1320 (INPA, UEC)
<i>Utricularia cucullata</i> A.St.-Hil. & Girard	sub	N, NE, CO, SE, S	F	SM Costa 712 (INPA, UEC)
<i>Utricularia foliosa</i> L.	sub	N, NE, CO, SE, S	M&A, J&P, P, C, F, MJr	SM Costa 767 (INPA, UEC)
<i>Utricularia gibba</i> L.*	sub	N, NE, CO, SE, S	M&A, J&P, C, F, MJr	SM Costa 895 (INPA, UEC)
<i>Utricularia guyanensis</i> A.DC.*	pal	N, NO, CO	M&A, F, MJr	SM Costa 756 (INPA, UEC)
<i>Utricularia hispida</i> Lam.*	pal	N, NE, CO, SE	F	SM Costa 869 (INPA, UEC)
<i>Utricularia hydrocarpa</i> Vahl*	sub	N, NE, CO, SE, S	F	SM Costa 744 (INPA, UEC)
<i>Utricularia juncea</i> Vahl	pal	N, NE	F	SM Costa 746 (INPA, UEC)
<i>Utricularia longiciliata</i> DC.	pal	N	F	TDM Barbosa 1345 (INPA, UEC)
<i>Utricularia myriocista</i> A.St.-Hil. & Girard	sub	N, NE, CO, SE	M&A, C, F, MJr	SM Costa 740 (INPA, UEC)
<i>Utricularia nana</i> A.St.-Hil. & Girard*	pal	N, NE, CO, SE, S	F	SM Costa 699 (INPA, UEC)
<i>Utricularia olivacea</i> Wright ex. Girard*	sub	N, CO, SE, S	F	SM Costa 727 (INPA, UEC)
<i>Utricularia pusilla</i> Vahl	pal	N, NE, CO, SE	M&A, F, MJr	SM Costa 691 (INPA, UEC)
<i>Utricularia sandwithii</i> P. Taylor	pal	N	F	SM Costa 701 (INPA, UEC)
<i>Utricularia simulans</i> Pilg.	pal	N, NE, CO, SE	M&A, F, MJr	SM Costa 716 (INPA, UEC)
<i>Utricularia subulata</i> L.	pal	N, NE, CO, SE, S	M&A, F, MJr	SM Costa 706 (INPA, UEC)
<i>Utricularia triloba</i> Benj.	pal	N, NE, CO, SE, S	M&A, F, MJr	SM Costa 709 (INPA, UEC)
<i>Utricularia viscosa</i> Spruce ex Oliver	pal	N, NE, CO	F	SM Costa 719 (INPA, UEC)
LINDERNIACEAE (1/1)				
<i>Lindernia diffusa</i> (L.) Wierst.	pal	N, NE, CO, SE, S	F, MJr	TDM Barbosa 1250 (INPA, UEC)
LYTHRACEAE (1/1)				
<i>Cuphea</i> cf. <i>gracilis</i> Kunth ^{&}	pal		F	TDM Barbosa 1132 (UEC)

SPECIES	Life form	Occurrence in Brazil	Also listed at	Selected Vouchers
MAYACACEAE (1/2)				
<i>Mayaca fluviatilis</i> Aubl.	pal, sub	N, NE, CO, SE, S	F, MJr	SM Costa 873 (INPA, UEC)
<i>Mayaca longipes</i> Mart. ex Seub.	pal, sub	N, NE, CO, SE	F, MJr	TDM Barbosa 1099 (INPA, UEC)
MELASTOMATACEAE (7/10)				
<i>Acisanthera crassipes</i> (Naudin) Wurdack	pal, emer	N, NE, CO	F	MJR Rocha 747 (BHCB)
<i>Acisanthera tetrapeta</i> (Cogn.) Gleason	pal, emer	N	F	TDM Barbosa 1386 (INPA)
<i>Comolia microphylla</i> Benth.	pal	N	F	TDM Barbosa 1111 (INPA, UEC)
<i>Comolia villosa</i> (Aubl.) Triana	pal	N, NE	F, MJr	TDM Barbosa 1182 (INPA)
<i>Macairea lasiophylla</i> (Benth.) Wurdack *	pal	N	M&A, F	KG Cangani 160 (INPA)
<i>Pachyloma coriaceum</i> DC.	pal	N	F	R Goldenberg 1591a (INPA)
<i>Pachyloma hubertioides</i> (Naudin) Triana	pal	N	F	TDM Barbosa 1205 (INPA, UEC)
<i>Rhynchanthera grandiflora</i> (Aubl.) DC.	pal	N, NE, CO, SE	F, MJr	MK Caddah 871 (INPA, UEC)
<i>Siphanthera couvianii</i> Wurdack & *	pal		F	SM Costa 926 (INPA, UEC)
<i>Tibouchina aspera</i> Aubl.	pal	N, NE, CO	M&A, F, MJr	TDM Barbosa 1317 (INPA, UEC)
MENYANTHACEAE (1/1)				
<i>Nymphoides indica</i> (L.) Kuntze	fleav	N, NE, CO, SE, S	M&A, C, F, MJr	TDM Barbosa 1101 (UEC), GA Gomes-Costa 114 (INPA)
MOLLUGINACEAE (1/1)				
<i>Gliricis radicans</i> (Ruiz & Pav.) Rohr.	pal	N, NE, CO, SE, S	F	SM Costa 1063
NYMPHAEEACEAE (1/3)				
<i>Nymphaea amazonum</i> Mart. & Zucc.*	fleav	N, NE, CO, SE, S	J&P, F	MCE Amaral 2015/19 (INPA)
<i>Nymphaea gardneriana</i> Planch.	fleav	N, NE, CO, SE, S	C, F, MJr	TDM Barbosa 1229 (UEC)
<i>Nymphaea rudgeana</i> G.Mey.	fleav	N, NE, SE, S	M&A, F, P, MJr	SM Costa 815 (UEC)
OCHNACEAE (1/3)				
<i>Sauvagesia erecta</i> L.	pal	N, NE, CO, SE, S	M&A, F, MJr	TDM Barbosa 1102 (UEC)
<i>Sauvagesia ramosa</i> (Gleason) Sastre	pal	N	F	TDM Barbosa 1335 (INPA, UEC)
<i>Sauvagesia sprengelii</i> A.St.-Hil.	pal	N, NE, SE	M&A, F, MJr	TDM Barbosa 1166 (INPA, UEC)
ONAGRACEAE (1/4)				
<i>Ludwigia hyssopifolia</i> (G.Don) Exell	pal, emer	N, NE, CO, SE, S	F, MJr	SM Costa 973 (INPA, UEC)

SPECIES	Life form	Occurrence in Brazil	Also listed at	Selected Vouchers
<i>Ludwigia leptocarpa</i> (Nutt.) H.Hara	pal, emer	N, NE, CO, SE, S	J&P, F, MJr	TDM Barbosa 1410 (INPA, UEC)
<i>Ludwigia nervosa</i> (Poir.) H.Hara	pal, emer	N, NE, CO, SE, S	M&A, F, MJr	TDM Barbosa 1234 (INPA, UEC)
<i>Ludwigia sedoides</i> (Humb. & Bonpl.) H.Hara	sub, fleav	N, NE, CO, SE	M&A, C, F, MJr	SM Costa 764 (INPA, UEC)
ORCHIDACEAE (8/10)				
<i>Catasetum discolor</i> (Lindley) Lindley	pal	N, NE, SE	(vide Pessoa et al. 2015)	(vide Pessoa et al. 2015)
<i>Cleistes rosea</i> Lindl.	pal, emer	N, NE, CO, SE, S	M&A, F	SM Costa 1184 (INPA, UEC)
<i>Cleistes tenuis</i> (Reichenbach f. ex Grisebach) Schlechter	pal	N, NE, CO, SE, S	(vide Pessoa et al. 2015)	(vide Pessoa et al. 2015)
<i>Duckeella pauciflora</i> Garay ^{ys}	pal	N	F	TDM Barbosa 1424 (INPA, UEC)
<i>Epidendrum orchidiflorum</i> Salzmann ex Lindley	pal	N, NE, SE	(vide Pessoa et al. 2015)	(vide Pessoa et al. 2015)
<i>Epistephium lucidum</i> Cogn.	pal	N, NE, CO, SE	F	E Pessoa 742 (INPA)
<i>Epistephium parviflorum</i> Lindley	pal	N, CO	(vide Pessoa et al. 2015)	(vide Pessoa et al. 2015)
<i>Galeandra devoniana</i> M.R. Schomb. ex Lindl.	pal	N	F	TDM Barbosa 1270 (INPA, UEC)
<i>Habenaria schuackei</i> Barb. Rodt.	pal, emer	N, NE, CO, SE, S		TDM Barbosa 1309 (INPA, UEC)
<i>Nohauilliamsia pirarensis</i> (Reichenbach f.) M.W.Chase & Whittren	pal	N	(vide Pessoa et al. 2015)	(vide Pessoa et al. 2015)
OROBANCHACEAE (1/1)				
<i>Agalinis hispidula</i> (Mart.) D'Arcy	pal	N, NE, CO	F	FN Cabral 473 (UEC)
PLANTAGINACEAE (1/2)				
<i>Bacopa egensis</i> (Poepp.) Pennell*	pal, sub	N, CO	F, MJr	SM Costa 1061 (UEC)
<i>Bacopa reflexa</i> (Benth.) Edwall	sub	N, NE, CO	F, MJr	SM Costa 755 (INPA, UEC)
POACEAE (7/12)				
<i>Andropogon bicornis</i> L.	pal	N, NE, CO, SE, S	M&A, F, MJr	TDM Barbosa 1276 (UEC)
<i>Andropogon leucostachyus</i> Kunth	pal	N, NE, CO, SE, S	M&A, F	TDM Barbosa 1150 (UEC)
<i>Andropogon virgatus</i> Desv.*	pal	N, NE, CO, SE, S	M&A, F	TDM Barbosa 1261 (UEC)
<i>Axonopus fissifolius</i> (Raddi) Kuhlms.*	pal	N, NE, CO, SE, S	F	PL Viana 5207 (INPA)
<i>Axonopus pubivaginatus</i> Hent.	pal	N, NE, SE	F	TDM Barbosa 1072 (UEC)
<i>Echinoalaena inflexa</i> (Poir.) Chase	pal, emer	N, NE, CO, SE, S	F	TDM Barbosa 1183 (UEC)
<i>Oryza rufipogon</i> Griff.*	emer	N, CO	F, P	TDM Barbosa 1231 (UEC)
<i>Otachyrium grandiflorum</i> Send. & Soderstr.	pal	N, CO	F	TDM Barbosa 1062 (UEC)
<i>Otachyrium versicolor</i> (Döll) Henrard	pal	N, NE, CO, SE, S	F	TDM Barbosa 1109 (UEC)

SPECIES	Life form	Occurrence in Brazil	Also listed at	Selected Vouchers
<i>Paspalum cf. lacustre</i> Chase ex Swallen*	emer	N	F	TDM Barbosa 1245 (UEC)
<i>Paspalum repens</i> PB. Bergius	emer	N, NE, CO, SE, S	M&A, C, F, MJr	TDM Barbosa 1204 (UEC)
<i>Trichanthecium cyanescens</i> (Nees ex. Trin.) Zuloaga & Morrone	pal	N, NE, CO, SE, S	MJr	
POLYGALACEAE (1/5)				
<i>Polygala adenophora</i> DC.	pal	N, NE, CO	M&A, F, MJr	TDM Barbosa 1218 (INPA, UEC)
<i>Polygala appressa</i> Benth.	pal	N, NE	M&A, F, MJr	TDM Barbosa 1145 (INPA, UEC)
<i>Polygala longicaulis</i> Kunth	pal	N, NE, CO, SE, S	M&A, F, MJr	TDM Barbosa 1185 (INPA, UEC)
<i>Polygala trichosperma</i> Jacq.	pal	N, NE	F, MJr	SM Costa 954 (INPA)
<i>Polygala violacea</i> Aubl.	pal	N, NE, CO, SE, S	F	DM Cavalcanti 205 (INPA)
PONTERDERIACEAE (1/3)				
<i>cf. Eichhornia crassipes</i> (Mart.) Solms	float	N, NE, CO, SE, S	F, MJr	-
<i>Eichhornia diversifolia</i> (Vahl) Urb.	emer, sub, flav	N, NE, C, SE, S	M&A, F, MJr	TDM Barbosa 1187 (INPA, UEC)
<i>Eichhornia heterosperma</i> Alexander	emer, sub	N, NE, CO, SE	F	TDM Barbosa 1352 (INPA, UEC)
RAPATEACEAE (4/6)				
<i>Cephalostemon affinis</i> Körn.*	pal, emer	N, CO	F	TDM Barbosa 1256 (INPA, UEC)
<i>Duckea squarrosa</i> (Willd. ex Link) Maguire *	pal, emer	N	F	TDM Barbosa 1273 (INPA, UEC)
<i>Monotrema aemulans</i> Körn.*+	pal, emer	N, CO	F	SM Costa 882 (UEC)
<i>Monotrema bracteatum</i> Maguire &+	pal, emer		F	TDM Barbosa 1281 (INPA, UEC)
<i>Monotrema xyridoides</i> Gleason *	pal, emer	N	F	TDM Barbosa 1225 (INPA, UEC)
<i>Spathanthus bicolor</i> Ducke	pal, emer	N	F	TDM Barbosa 1297 (INPA, UEC)
RUBIACEAE (4/7)				
<i>Borreria alata</i> (Aubl.) DC.	pal	N, NE, CO, SE, S	F	TDM Barbosa 1190 (UEC)
<i>Borreria capitata</i> (Ruiz & Pav.) DC.	pal	N, NE, CO, SE, S	M&A, F	SM Costa 976 (UEC)
<i>Borreria verticillata</i> (L.) G.Mey.	pal	N, NE, CO, SE, S	M&A, F, MJr	SM Costa 976 (UEC), N Dávila 6309 (INPA)
<i>Declieuxia fruticosa</i> (Willd. ex Roem. & Schult.) Kuntze	pal	N, NE, CO, SE, S	F	TDM Barbosa 1131 (INPA, UEC)
<i>Penama galioides</i> (Kunth) Poir.	pal	N, CO	F	TDM Barbosa 1143 (INPA, UEC)
<i>Penama hirsuta</i> Aubl.	pal	N, NE, CO, SE	M&A, F	TDM Barbosa 1308 (UEC)
<i>Sipanea pratenis</i> Aubl.	pal	N, NE, CO, SE	M&A, F, MJr	TDM Barbosa 1178 (INPA, UEC)

SPECIES	Life form	Occurrence in Brazil	Also listed at	Selected Vouchers
SOLANACEAE (1/1)				
<i>Melananthes ulei</i> Carvalho [#]	pal	NE, CO	F	FN Cabral 392 (UEC)
VERBENACEAE (1/1)				
<i>Stachytarpheta angustifolia</i> (Mill.) Vahl *	pal	N, NE, SE	F, MJr	SM Costa 974 (INPA, UEC)
XYRIDACEAE (2/20)				
<i>Abolboda americana</i> (Aubl.) Lanj.	pal	N, NE, CO, SE	F	SM Costa 703 (INPA, UEC)
<i>Abolboda killipii</i> Lasser ⁺	pal	N	F	TDM Barbosa 1095 (INPA, UEC)
<i>Abolboda macrostachya</i> Spruce ex Malme	pal	N, CO	F	TDM Barbosa 1332 (INPA, UEC)
<i>Abolboda pulchella</i> Humb. & Bonpl.	pal	N, NE, CO, SE	F	TDM Barbosa 1346 (INPA, UEC)
<i>Xyris cryptantha</i> Maguire & L.B. Sm. ⁺	pal	N	F	SM Costa 704 (INPA, UEC)
<i>Xyris dilatatiscapa</i> Kral & Jans.-Jac. ^{+,s}	pal	N		Mota et al. (2015)
<i>Xyris fallax</i> Malme	pal	N, NE, CO, SE	F	SM Costa 741 (INPA, UEC)
<i>Xyris guianensis</i> Steud.	pal	N	F	NFO Mota 2313 (INPA, UEC)
<i>Xyris involucrata</i> Nees	pal	N	F	Mota et al. (2015)
<i>Xyris jupicai</i> Rich.	pal	N, NE, CO, SE, S	F, MJr	SM Costa 884 (INPA, UEC)
<i>Xyris laxifolia</i> Mart. [=X. <i>macrocephala</i> Vahl]	pal	N, NE, CO, SE, S	M&A, F, MJr	Mota et al. (2015)
<i>Xyris malmeana</i> L.B. Sm. ⁺	pal	N, NE, CO	F	SM Costa 778 (INPA, UEC)
<i>Xyris minima</i> L.B. Sm. & Downs	pal	N	F	TDM Barbosa 1442 (INPA, UEC)
<i>Xyris pumensis</i> Poepp. ex Kunth	pal	N, NE, CO	M&A, F, MJr	SM Costa 909 (INPA, UEC)
<i>Xyris savanensis</i> Miq.	pal	N, NE, CO, SE, S	M&A, F, MJr	SM Costa 784 (INPA, UEC)
<i>Xyris subglabrata</i> Malme	pal	N	F	TDM Barbosa 1217 (INPA, UEC)
<i>Xyris subuniflora</i> Malme	pal	N	F	TDM Barbosa 799 (INPA, UEC)
<i>Xyris surinamensis</i> Spreng.	pal	N	F	TDM Barbosa 1306 (INPA, UEC)
<i>Xyris uleana</i> var. <i>angustifolia</i> Lanj.	pal	N	F	SM Costa 753 (INPA)
<i>Xyris uleana</i> var. <i>uleana</i> Malme	pal	N, CO	F	SM Costa 800 (INPA)
<i>Xyris</i> sp.	pal	-		Mota et al. (2015)

genera and 37 families (Table 1; Figures 3–4). Nine species remain identified only at genus level or at species level but with doubtful status (cf./aff.).

The richest families are Cyperaceae (45 spp.), Lentibulariaceae (25 spp.) and Xyridaceae (20 spp.) and the richest genera are *Utricularia* L. (Lentibulariaceae; 22 spp.), *Xyris* L. (Xyridaceae; 16 spp.) and *Rhynchospora* Vahl (Cyperaceae; 15 spp.).

We recorded six new occurrences and one probable new occurrence for Brazil, two new occurrences for the northern region and 21 new occurrences for the state of Roraima. Our list presents six new occurrences for Brazil, namely: *Rhynchospora maguireana* T. Koyama and *Scleria amazonica* Camelbeke, M.Strong & Goetgh. (Cyperaceae), *Drosera kaieurensis* Brumm.-Ding. (Droseraceae), *Croton subseratus* Jabl. (Euphorbiaceae), *Siphanthera cowanii* Wurdack (Melastomataceae) and *Monotrema bracteatum* Maguire (Rapateaceae); and a probable new occurrence: *Cuphea* cf. *gracilis* Kunth (Lythraceae). Additionally, there are two new records for the northern Brazilian region (*Aeschynomene scabra* G.Don and *Eichhornia heterosperma* Alexander).

All life forms were registered in the VNP (see Table 1), with 20% of the species included in more than one category. Palustrine plants encompass 175 species (approximately 85% of species). The most species-rich families are Cyperaceae (41 spp.), Xyridaceae (21 spp.) and Lentibulariaceae (17 spp.), all of them common in water-logged soils. The emergent and submerged categories presented 43 and 23 species, respectively, and eight species rooting in mud and with floating leaves; while among the free-floating plants solely two species were recorded (*Pistia stratiotes* L. and cf. *Eichhornia crassipes* (Mart.) Solms). Taking into account only the submerged plants, Lentibulariaceae was the most species-rich family, with eight species of *Utricularia*. Each of the other families with plants adapted to submersed conditions had between one and three species. Among the families with emergent plants, Cyperaceae was the most diverse, with 16 species distributed in seven genera.

As regards A&P angiosperms listed here, only 13 species appear to be restricted to white-sand savannas (see Table 1), most of these also recorded for areas in the Guiana Shield. Approximately 56 species occur solely in the northern region of Brazil, and five of them are only found in Roraima state.

Discussion

Identification of A&P plants occurring at VNP

On the identification of A&P plants occurring at VNP, it required the examination of several references, *online* collections and specialists. This correct identification is important as it allows the accurate list and comparison of subsampled vegetation (white-sand savannas; Vicentini 2004) and Amazon area (Hopkins 2007) with other areas and vegetation.

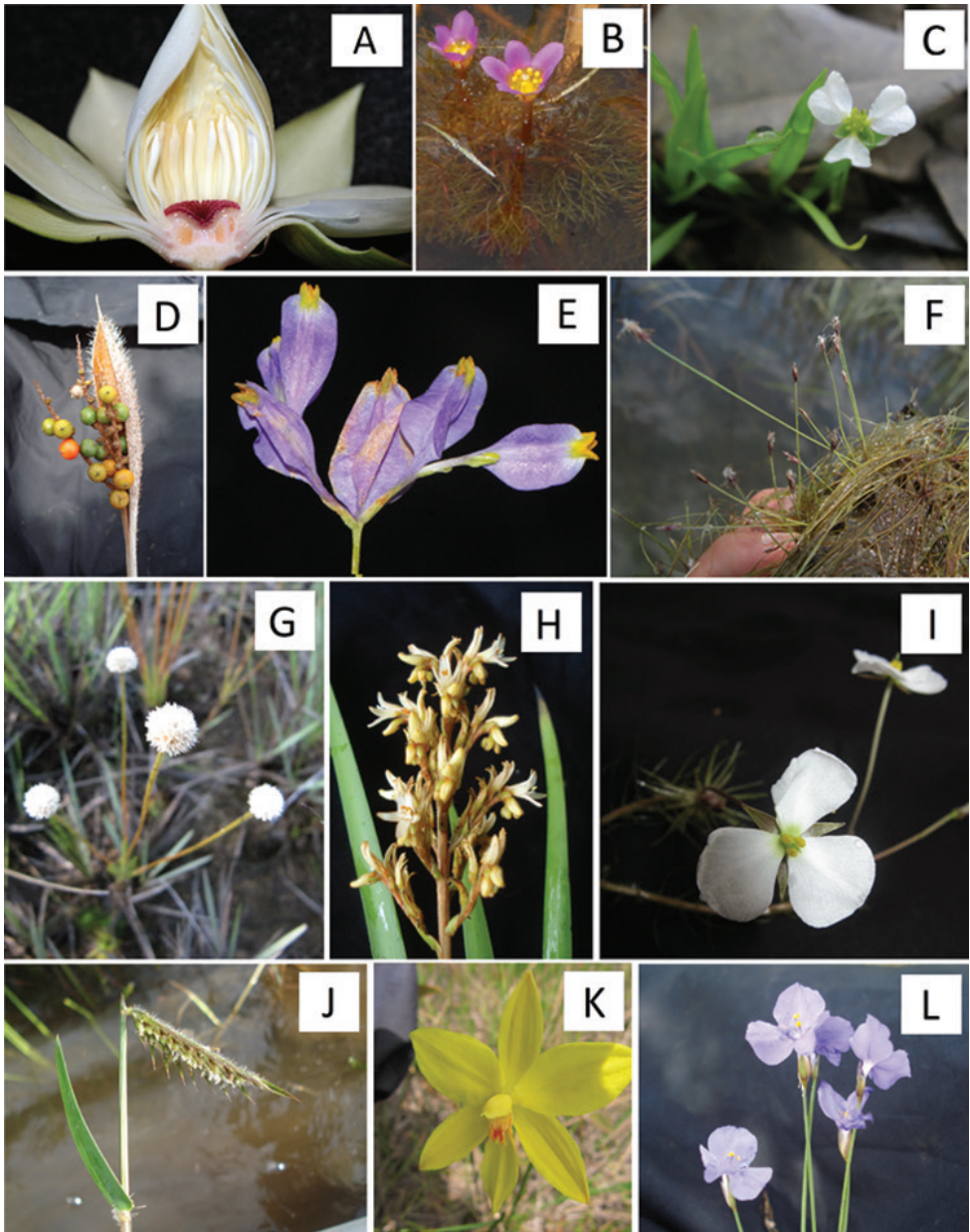


Figure 3. Wetland basal angiosperms and monocots of Viruá National Park (selected examples). **A** *Nymphaea amazonum* Mart. & Zucc. **B** *Cabomba furcata* Schult. & Schult. f. **C** *Helanthium tenellum* (Mart. ex Schult. & Schult. f.) Britton **D** *Bactris campestris* Poepp. **E** *Burmannia bicolor* Mart. **F** *Eleocharis fluctuans* (L.T. Eiten) E.H. Roalson & C.E.Hinchliff **G** *Syngonanthus fenestratus* Hensold **H** *Schiekia orinocensis* (Kunth) Meisn. **I** *Mayaca longipes* Mart. ex Seub. **J** *Echinolaena inflexa* (Poir.) Chase **K** *Duckeella pauciflora* Garay **L** *Abolboda pulchella* Humb. & Bonpl.

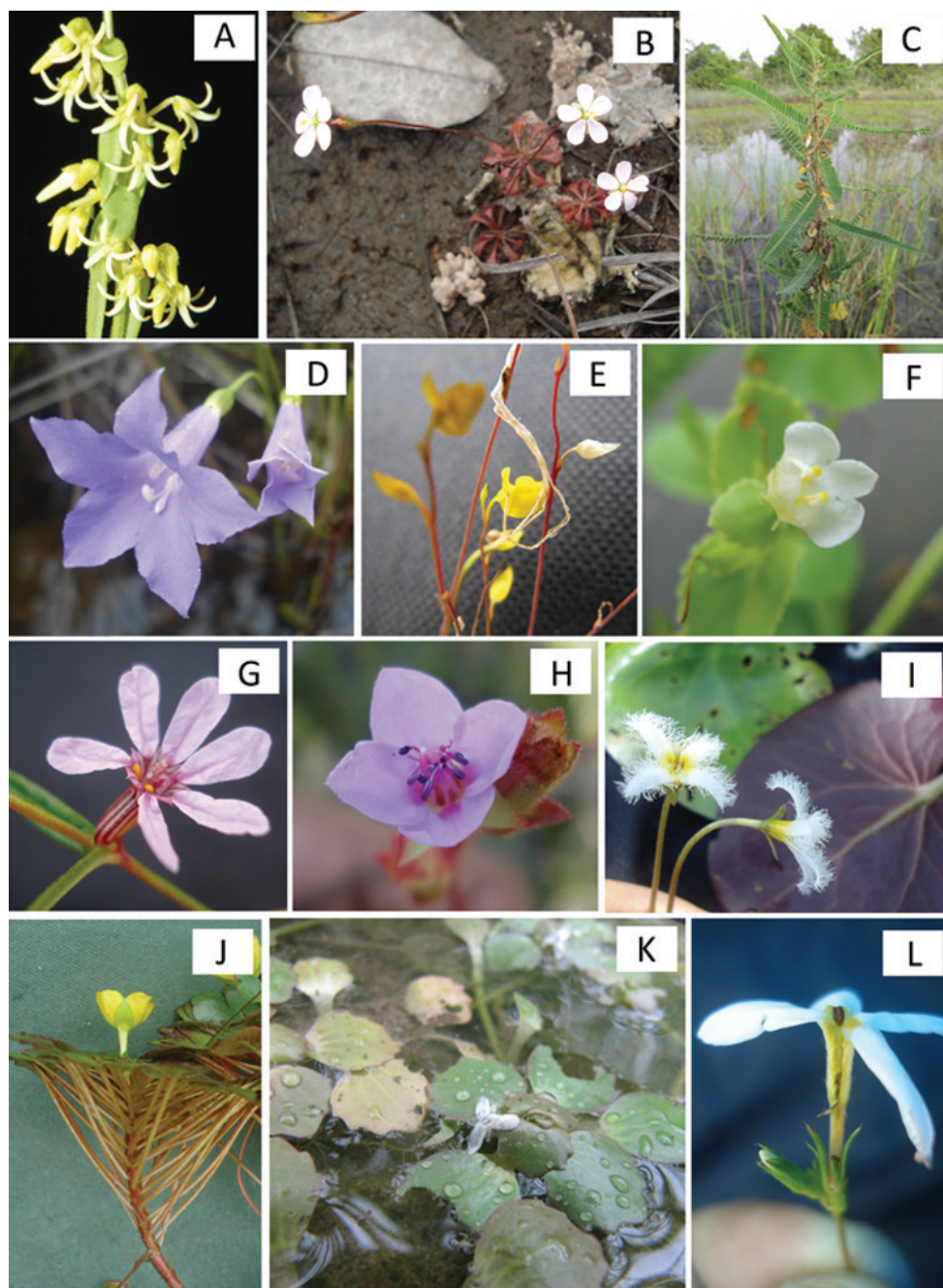


Figure 4. Wetland eudicots of Viruá National Park (selected examples). **A** *Cynanchum guanchezii* Morillo **B** *Drosera kaieteurensis* Brumm.-Ding. **C** *Aeschynomene scabra* G.Don **D** *Irlbachia pratensis* (Kunth) L.Cobb & Maas **E** *Utricularia chiribiquetensis* Fernandez-Pérez **F** *Lindernia diffusa* (L.) Wettst **G** *Cuphea* cf. *gracilis* Kunth **H** *Acisanthera tetraptera* (Cogn.) Gleason **I** *Nymphoides indica* (L.) Kuntze **J** *Ludwigia sedoides* (Humb. & Bonpl.) H.Hara **K** *Bacopa egensis* (Poepp.) Pennell **L** *Sipanea pratensis* Aubl.

We still are studying some specimens of VNP, but especially when they belong to large genera, such as *Eleocharis* R.Br. (Cyperaceae), this process can take considerable time in the gathering of scattered and sometimes hardly accessible references.

We observed a population of cf. *Eichhornia crassipes* in the VNP but all individuals were sterile. The identification of sterile specimens is sometimes imprecise but floating islands of *Eichhornia crassipes* were observed in the Branco River (near the urban area of Caracará and out of the VNP) and the sterile population shown the aerenchymatous petiole characteristic of this species (Horn 2004). So we decided to list it as cf. *E. crassipes* (Table 1).

A peculiar case of complex identification in the VNP is the case of *Bacopa egen-sis* (Poepp.) Pennell (currently in Plantaginaceae). The identification to genus or even family was difficult, as the floras and taxonomical works consulted did not include the respective genus or contained errors in the identification keys and/or inaccurate descriptions. Not even the description provided by Souza and Giulietti (2009) encompass the morphological variation exhibited in the specimens of the VNP (K4 C3 A3). Specialists previously classified this species in the genus *Hydranthelium* Kunth and it does not fit in most descriptions of Scrophulariaceae s.l. or Plantaginaceae or even *Bacopa*.

New occurrences and endemisms in white-sand savannas/“campinaranas”

Our data indicated new occurrences to both Roraima state and Brazil. It includes species previously registered for the Guiana Shield, an adjacent phytogeographical unit to the north (Funk et al. 2007).

Additionally, at least seven species among the new registers to Roraima are widely distributed in other Brazilian regions, e.g., *Syngonanthus cuyabensis* (Bong.) Giul., Hensold & L.R. Parra (Eriocaulaceae), *Utricularia gibba* L., *U. hydrocarpa* Vahl, *U. nana* A.St.-Hil. & Girard (Lentibulariaceae), *Nymphaea amazonum* Mart. & Zucc. (Nymphaeaceae), *Andropogon virgatus* Desv. and *Axonopus fissifolius* (Raddi) Kuhlman. (Poaceae). The two new records to northern Brazil, *Aeschynomene scabra* and *Eichhornia heterosperma*, are widely distributed species (Amaral 2013, Lima and Oliveira 2013) that simultaneously occur in the Guiana Shield and other Brazilian regions (Funk et al. 2007, Forzza et al. 2015). The delay of their register may be caused by the insufficient collection effort in Amazonia region.

Among A&P plants, only a few *taxa* are unique to a vegetation type and/or present restricted distributions (Sculthorpe 1967), and rare species generally display larger distribution areas than those of rare terrestrial species (Santamaría 2002); although Podostemaceae is an exception worth mentioning as they are commonly endemic to a single basin or even a single waterfall (Cook and Rutishauser 2007). Endemic species may occur in white-sand savannas, the predominant vegetation type in the VNP, and such species are probably spread in the numerous isolated “islands” of this vegetation type within rainforest (Anderson 1981).

There is no species endemic to the VNP and the endemic species of white-sand savannas belonging to the A&P plants that we listed here are not restrict to Brazilian

territory and occur in other northern South American countries (such as Venezuela, Guyana and/or Colombia) (Table 1). Additionally, in Brazil the apparent restricted distribution in Roraima state may be in part the result of insufficient collections in white-sand savannas. We identified some specimens collected in this phytophysognomies in Amazonas state and not yet deposited in any herbaria, which belong to such endemic species. In fact, endemic species of white-sand savannas were recently listed in other studies of the Viruá National Park (Cabral 2011, Dávila 2011, Azambuja 2012, Cangani 2012, Pessoa et al. 2015, Mota et al. 2015). Other *taxa* with a more restricted distribution are families, genera or species with concentrated richness or exclusive occurrence in northern South America, or only in the Guiana Shield, e.g. Rapateaceae, *Abolboda* Bonpl. and *Utricularia benjaminiana* Oliv.

Life forms

We registered in the VNP all life forms usually recognized to these plants (Cronk and Fenessy 2001, Chambers et al. 2008), namely: palustrine (e.g. Xyridaceae), emergent (e.g. *Montrichardia arborescens*), with floating leaves (e.g. *Nymphaeae* spp.), free floating (e.g. *Pistia stratioides*) and submerged (e.g. *Mayaca* spp.). It is known that the number of species decreases towards strictly submerged plants (Barrett et al. 1993), as observed in our data.

Gribel et al. (unpublished data) reported the occurrence of species belonging to two genera of free floating plants in the “buritizais” in the study area (*Wolffia* Horkel ex Schleid. and *Spirodela* Schleid.), but we did not find specimens of these genera during our expeditions or in herbaria we consulted. Free-floating species depend on the nutrients dissolved in the water column (Cronk and Fenessy 2001) and the low richness at VNP may be due to the *igapó* characteristics attributed to the local waterbodies (low inorganic nutrient concentrations) (ICMBio 2014, Junk et al. 2011).

Floristic connections

Concerning to the floristic comparisons, 189 species listed here were also found in Funk et al. (2007); 69 species in Moura-Júnior et al. (2015); 50 species in Miranda and Absy (1997); 13 species in Conserva et al. (2008); nine in Junk and Piedade (1993) and four in Piedade et al. (2010) (Table 1).

There are relatively few floristic lists for wetland plants in the Amazon region (Piedade et al. 2010) and in particular the northern Brazilian region remains strongly undercollected (Hopkins 2007, Schulman et al. 2007, Piedade et al. 2010). This situation makes it difficult or even impossible for us to compare our results with other works and probably turns artifacts caused by low sampling into apparent patterns (Hopkins 2007, Piedade et al. 2010).

Another study focusing on A&P plants also carried out in the VNP is yet unpublished (Paiva 2012). In it, the collecting effort was concentrated in the PPBio

(Biodiversity Research Program) grid, in a more forested area within the national park, and in an area of hydromorphic open white-sand savanna near the “Estrada Perdida” road. The authors listed 19 species, some of them present in our list. The material was identified only in part and at genus level and at the time of our visit to the herbaria in Roraima, the vouchers of Paiva (2012) were not available yet. Since we could not analyze those specimens, the different taxa there listed do not appear in our list, so further comparisons could not be made.

The similarity of the aquatic and palustrine flora of the Viruá National Park with that of the Guiana Shield is evident, only 17 species of our list are absent in Funk et al. (2007) list. One must consider the geographic proximity between the two areas. Additionally, both have common limiting conditions for many plant species, mainly the nutrient-poor soils (Janzen 1974, Prance and Schubart 1978, Anderson 1981, Steyermark et al. 1995, Funk et al. 2007).

Junk et al. (2011) classified the rivers of the study area, including the sediment-rich Branco River, as black- or clear-water due to the low levels of dissolved nutrients. The *igapó* and *várzea* differ regarding their floristic composition and as to their ecological patterns (Prance 1979, Klinge 1983, Pires and Prance 1985, Piedade et al. 2010, Junk et al. 2011). Prance (1979) refers to the exclusive occurrence of some species to each vegetation type: e.g. *Bombax munguba* Mart. (Malvaceae), *Couroupita subsessilis* Pilg. (Lecythidaceae) and *Hevea brasiliensis* Muell. (Euphorbiaceae) to *várzea* areas; and *Couepia paraensis* (Mart. & Zucc.) Benth. and *Licania apetala* (E. Mey.) Fritsch (Chrysobalanaceae) and *Tabebuia barbata* (E. Mey.) Sandw. at *igapó* areas.

Two species reported in our list, namely *Bacopa egensis* (otherwise collected in the Solimões River, in Central America – including in rice-fields – and even in swamps near New Orleans, Louisiana; Christenhusz 2014) and *Glinus radiatus* (Ruiz & Pav.) Rohr. (sometimes recorded as weed) are supposedly associated with nutrient-rich habitats. These species were only collected in a lake less than 1 km from the margin of the Branco River (*Ano Bom* lake, which receives floodwater from the Branco River periodically), in an area with gray clay soil. Junk et al. (2011) state that the water of the Branco River, which resembles a white-water river, has low nutrient status and it is thus chemically closer to a clear-water river. The presence of these two species suggests that the Branco River may be richer in nutrients than a clear-water river.

The comparison of our list with that of an area of *várzea* near Manaus (Junk and Piedade 1993) illustrates some of these differences between nonarboreal *Várzea* and *Igapó* areas; only a few species are common to both areas and in the *várzea* vegetation Poaceae and Araceae s.l. (predominantly Lemnoideae) are the richest families of wetland species. Another study of wetland plants at the Amazonas/Solimões River interface also revealed a low number of species in common with the VNP (Conserva et al. 2008). However, both lists (Junk and Piedade 1993, Conserva et al. 2008) are based on expeditions made during the terrestrial phase (dry season), to facilitate access to the localities, influencing the results. Thus, there is an increasing richness of weedy species not necessarily adapted to wetland conditions in both inventories.

Few studies have been carried out in areas of *igapó* that focus on the diversity of herbaceous and subshrubby aquatic and palustrine plants (Piedade et al. 2010). Lopes et al. (2014) present a floristic analysis of A&P plant genera in six river systems with *igapó* characteristics in the Amazonas state. They listed 25 families and 63 genera, from which 15 families and 24 genera occur in the Viruá National Park (Lopes et al. 2014). Similarly to the pattern observed by Lopes et al. (2014), Cyperaceae is richer than Poaceae in the VNP. Those authors did not provide a species list and comparisons are not possible.

Indirectly, Piedade et al. (2010) mention four species to *igapó* areas: *Oryza perennis* Moench, *Nymphaea rudgeana* G. Mey., *Utricularia foliosa* L. and *Cabomba aquatica* Aubl. As regards the yellow-flowered *Cabomba* Aubl. with four tepals that occurs in the VNP and in the Jufari River (see Piedade et al. 2010), we identified this species as *Cabomba schwartzii* Rataj. Currently, specialists list this species as a synonym of *C. aquatica*, typically with six tepals (Forzza 2015). The name *Oryza perennis* is doubtful and specialists will soon submit a proposal to reject it (Robert Soreng, pers. comm.). The specimens named *O. perennis* in Amazonia and the Guianas are probably *O. rufipogon* Griff. Therefore, we also recorded all four species mentioned by Piedade et al. (2010) for the Jufari River in the VNP; all are widely distributed species.

At northern Roraima there is other non-forest vegetation with different abiotic conditions enclosed in the matrix of Amazonian rainforest, the savannas (ICMBio 2014; IBGE 2012). Again, we know little regarding A&P plants in the savannas of Roraima and must take some care when making comparisons with the few works published, such as considering the need for a revision of the identifications published in older lists. The limitations of useful taxonomic literature, faced especially before the publication of the Flora of the Venezuelan Guayana, were considerable and sometimes researchers vaguely delimited study areas.

The floristic survey published by Miranda and Absy (1997) gathers data from various previously published inventories and results of the author's collections in the savanna region of Roraima, being the most complete list available to this area. It contains nearly 300 species: c. 30% are from wetlands and of these, 1% in strictly aquatic habitats. We herein recorded 50 of these species for the Viruá National Park, mostly species with a large geographical distribution. More recent lists of aquatic and palustrine species from Roraima state are unpublished (Neves 2007, Paiva 2012), thus only presenting a low number of more widely distributed species.

In the updated checklist of macrophytes from northern Brazil, that is based on previous lists plus recent data collected by the authors and data contained in the SpeciesLink and “*Lista da Flora do Brasil*” platforms, Júnior et al. (2015) listed about 540 spp. of A&P plants, among those species only 68 are in common with our list (Table 1). As their list probably gathers information from *Várzea* and *Igapó* areas with no distinction, useful discussions cannot be made at this moment. Anyway, some care must be taken as their list was based on information of the SpeciesLink platform, (according to Moura Júnior et al. 2015), where not all specimens are correctly identified. The criterion for the inclusion of the species used by those authors is not clear. Similarly, though the “*Lista da Flora do Brasil*” is a great source of information about species of

the Brazilian flora (as cited by Moura Júnior et al. 2015), it is still incomplete and with considerable data gaps for some taxa and geographical regions, such as aquatic and palustrine species and northern Brazil.

Conclusions and future studies

Despite the need for more collecting effort in the inner parts of the VNP, its flora of aquatic and palustrine herbaceous and subshrubby angiosperms is clearly connected to the flora of the Guiana Shield, an adjacent phytogeographical region to the north and geologically related to the origin of white-sand savannas, the predominant physiognomy in the protected area studied here.

Only the INPA herbarium held old specimens from the studied area and although we found some bibliography concerning wetland plants of the region, publications are scattered or the most complete refer mainly the Venezuelan and/or Guiana territory. A greater collecting effort and the revision of herbarium specimens are essential to allow for a meaningful evaluation of the similarities and differences between the white-sand savannas and other savanna areas of the Amazon. Reasonably complete lists of aquatic and palustrine plants in areas influenced by *igapó* rivers, white-sand savannas and other savannas in the Amazon region may also uncover floristic, biogeographical, evolutionary and ecological patterns currently obscured by the inadequate collection status.

To allow for the identification of the species here listed, our group is currently producing keys (including interactive multi-access keys), descriptions with images, taxonomic comments, geographical distribution and field observations of the listed *taxa*. We will provide these resources shortly, in the format of an eFlora on a website about the Viruá National Park (Costa et al. in prep.).

Acknowledgements

This work is part of first author's master thesis and was financed by the programs PNADB (Programa Nacional de Apoio ao Desenvolvimento da Botânica) and PRO-CAD (Programa Nacional de Cooperação Acadêmica). The first author's scholarship was granted by CAPES (Coordenação de Aperfeiçoamento de Pessoal de Nível Superior) and CNPq (Conselho Nacional de Desenvolvimento Científico e Tecnológico) and the Plant Biology Program (Institute of Biology – UNICAMP), MCEA is a CNPq research fellow. We are truly grateful to the staff of the Viruá National Park, represented by Antônio Lisbôa (director of the protected area) and to Mike Hopkins (INPA) and Sr Chico, without whom this work would have been impossible. Additionally, we thank the botanists studying in the Viruá National Park concomitantly and specialists who helped with the identification and/or confirmation of species in their groups, namely: Marccus Alves (Cyperaceae), Rosemeri Morokawa (Apocynaceae), Marcelo Monge Egea (Asteraceae), Ana Paula Fortuna (Leguminosae), Nállarett Dávila (Rubi-

aceae), Gisele Oliveira and Nara Mota (Xyridaceae), Nancy Hensold (Eriocaulaceae), Andrew Henderson (Arecaceae), Kátia Cangani (Melastomataceae), and Ricarda Riina (Euphorbiaceae). We thank Cynthia Sothers, Royal Botanic Gardens, Kew, for correcting the English version of the manuscript.

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A revision of the genus *Osmoxylon* (Araliaceae) in Palau, including two new species

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Academic editor: Mark Watson | Received 12 May 2015 | Accepted 10 November 2015 | Published 12 January 2016

Citation: Costion CM, Plunkett GM (2016) A revision of the genus *Osmoxylon* (Araliaceae) in Palau, including two new species. *PhytoKeys* 58: 49–64. doi: 10.3897/phytokeys.58.5292

Abstract

Osmoxylon Miq. (Araliaceae) is revised for Palau, Micronesia including descriptions of two new taxa *Osmoxylon leidichii* Costion, **sp. nov.** and *Osmoxylon ngardokense* Costion, **sp. nov.** Full descriptions are provided for all four Palau species, along with diagnostic field keys.

Keywords

Pacific Islands, taxonomy, Asteriids, Apiales

Introduction

Osmoxylon Miq. (Araliaceae) is a genus of rainforest trees and shrubs from southeastern Asia and the western Pacific (Philipson 1979; Frodin and Govaerts 2003). All of the 60 currently recognized species are characterized by large umbelliform panicles composed of several to many three-branched inflorescence units. Each inflorescence unit terminates in a stalked head or umbellule that develops sterile baccate “pseudo-fruits” and two lateral stalked heads or umbellules with fertile bisexual flowers and fruits. Other characteristic features of the genus include ligule-shaped stipules that clasp the stem and conspicuous rings or crests that circle or spiral around the petiole base. Like most araliads, the calyx is inconspicuous, forming a highly reduced rim around the inferior ovary, but the genus is unusual in the family in that all species have fused or united petals, forming a distinctively

tubular corolla. The genus has not received a modern comprehensive revision, but several regional treatments of *Osmoxylon* have made important contributions to its taxonomy from Malesia (Philipson 1979; Frodin 1998), New Guinea (Philipson 1995), and the Solomon Islands (Conn and Frodin 1995), and included the transfer of *Boerlagiodendron* Harms to *Osmoxylon* (see Philipson 1976; Frodin 1998). The highest species diversity for the genus occurs in the Philippines (17–19 spp.). Its range extends north to Taiwan (1), east into the Caroline and Marianna Islands (4) and south to the Wallacea region of Indonesia (11). From Wallacea its distribution extends west only to Borneo (2) but eastward across New Guinea (11) and the Solomon Islands (14) to Vanuatu (1).

Three species are currently recognized in Palau: *Osmoxylon oliveri* Fosberg & Sachet, *O. pachyphyllum* (Kaneh.) Fosberg & Sachet, and *O. truncatum* (Kaneh.) Fosberg & Sachet. The first record of the genus in the archipelago seems to date from the Japanese era, with a collection made in 1929, as recorded by Kanehira (1931) and identified as *Boerlagiodendron pulcherrimum* (Vid.) Harms. This species was originally described in *Osmoxylon* by Fernández-Villar (1880) based on material from the Philippines, but later transferred to Harms' (1894–1897) segregate genus. Shortly thereafter, Kanehira (1934) described two additional species, *B. truncatum* Kaneh. and *B. pachyphyllum* Kaneh. While Palau was under the administration of the United States, all three species were transferred to *Osmoxylon* by Fosberg and Sachet (1980), following Philipson's (1976, 1979) treatment of the genus in Malesia. In the same publication, Fosberg and Sachet segregated the Palauan material assigned to *B. pulcherrimum* (otherwise endemic to the Philippines) as a distinct species, *Osmoxylon oliveri*.

All three currently recognized species are known to occur on Palau's largest island, Babeldaob. *Osmoxylon truncatum* is only known from Babeldaob, but both *O. oliveri* and *O. pachyphyllum* have hitherto also been recorded from Palau's limestone islands. Recent collections, however, provide evidence that specimens identified as *O. pachyphyllum* from Palau's aforementioned islands represent a distinct, undescribed species and that the original concept of *O. truncatum* requires revision. Furthermore, another new species of *Osmoxylon* was recently discovered while establishing a forest-dynamics plot on Babeldaob. Herein, we here describe these two new species and combine the two previously known species *O. oliveri* and *O. truncatum*. A dichotomous key to the four known members of the genus in Palau is provided with a list of diagnostic characters for each species so they may be more easily distinguished by non-experts. These taxa tend to be encountered infertile in the field, resulting in great confusion in their identification, and we therefore provide two separate diagnostic keys, one based solely on vegetative material and a second for fertile collections.

Key to vegetative material of the Palau species of *Osmoxylon*

- 1 Leaf lobes 5–9.....2
- 2 Leaf lobes 5–7; stipules glabrous, strongly folded or recurved with tip sharp to the touch; teeth exserted or protruding from margin ***O. pachyphyllum***

- 2' Leaf lobes 7–9; stipules with tannish pubescence, clasping stem, flattened; teeth inserted, each tooth located within a crenulation in the margin..... *O. leidichii*
- 1' Leaf lobes 9–15..... **3**
- 3 Leaf lobes 9–11; stipules entire, glabrous; each prominent secondary vein branched, terminating in 1 or 2 serrations; junction of midrib and secondary veins nearly perpendicular, secondary veins then curving to a 30–45° angle... *O. nardokense*
- 3' Leaf lobes 11–15; stipules with distinct teeth or ciliate crests, more or less glabrous; prominent secondary veins branched, terminating in 2 or 3 serrations; junction of midrib and secondary veins at 30–45° angle *O. truncatum*

Key to fertile material of the Palau species of *Osmoxylon*

- 1 Inflorescence < 20 cm diameter, < 25 flowers or fruits per fertile umbellule **2**
- 2 Fertile umbellules 20–30 per inflorescence, borne on peduncles that are not distinctly jointed; fertile fruits globose, c. 20 per umbellule *O. leidichii*
- 2' Fertile umbellules 12–15 per inflorescence, borne on distinctly jointed peduncles, fertile fruits oblong in outline, angled and flattened, 3–5 per umbellule *O. pachyphyllum*
- 1' Inflorescence c. 20–30 cm in diameter, > 25 flowers or fruits per fertile head/umbellule..... **3**
- 3 Flowers 20–40 per umbellule, borne on minute pedicels; fertile fruits distinctly globose, shiny dark purplish-black *O. ngardokense*
- 3' Flowers 45–80 per head, sessile at anthesis, borne on a cone-shaped receptacle, pedicels form as fruits mature; fertile fruits obpyramidal (corn-kernel shaped), white-green maturing to dull purple from apex toward the base ... *O. truncatum*

Taxonomic treatment

Osmoxylon leidichii Costion, sp. nov.

urn:lsid:ipni.org:names:77151879-1

Fig. 1

Boerlagiodendron pachyphyllum Kaneh. p.p., Bot. Mag. Tokyo, 48: 401, 1934

Syntype: Palau. Aimeliik: 1933, R. Kanehira 2452

Type. Palau. Koror: Ngeremdiu Beach, 07°15'20.22"N, 134°26'37.98"E, 18m, 6 Jun 2014 (fr), C. Costion 3711 (holotype: NY; isotype: US, BNM).

Description. Small to medium sized tree, 10–12 m tall, branched. Leaf blades palmately lobed, up to 45 cm long and wide, glabrous, with 7–9 rhombic lobes; mar-

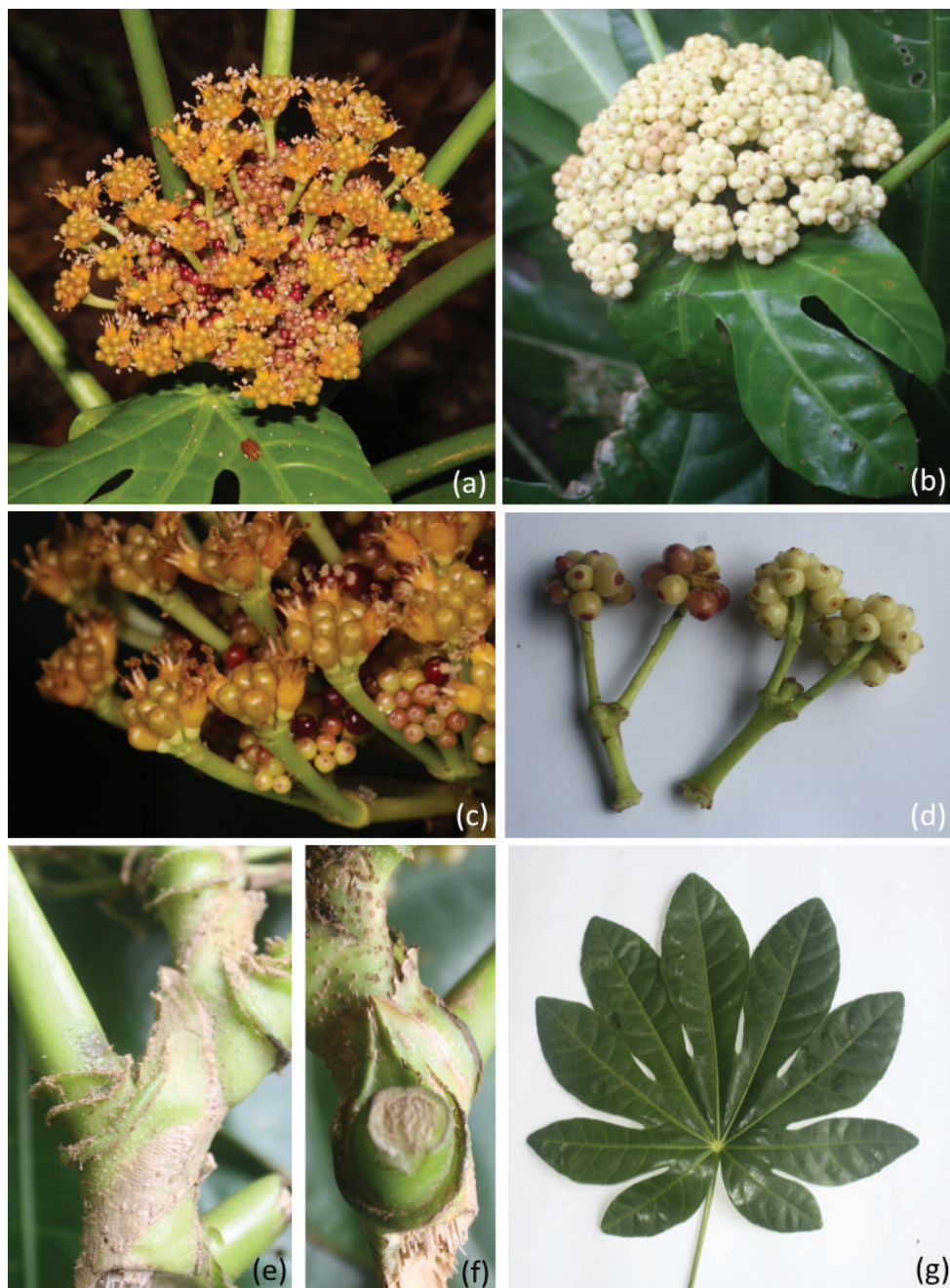


Figure 1. *Osmoxylon leidechii* **a** compound inflorescence with flowers **b** compound inflorescence with fruits **c** fertile flowers and sterile fruits **d** individual inflorescences with fruits **e** petiolar stipule side view and stipule crests **f** petiolar stipule overhead view **g** leaf.

gin with serrations minute and distinctly inserted or in tiny indentations of the blade, barely exceeding the margin itself, only one per secondary vein; prominent secondary veins 7 or 8 per lobe, meeting the mid-rib at a 30–45° angle; petioles up to 50 cm in length; petiolar crests 1–4, circular, re-curved, entire, with tannish pubescence along margins; stipule flattened and appressed to the stem, broadly attenuate to the apex, fleshy (not stiff), with brown flakey or papery margins and brownish pubescence, tip soft to touch, not firm. Inflorescence 10–15 cm in diameter, primary axis bearing 20–30 secondary inflorescence units, secondary axis (from primary axis to the point where the lateral fertile umbellules are attached) c. 2 cm long, with c. 30 pinkish to crimson, baccate pseudo-fruits, each 2 mm long and 2–3 mm in diameter; peduncles c. 3 cm long, light green, not distinctly jointed. Fertile flowers 10–20 per umbellule, each with a yellowish, fused or united, cup-shaped calyx, c. 2 mm long; corolla tube bright orange, 5 or 6 lobed, 3 mm long; stamens alternate to the petal lobes, strongly exserted; ovary inferior, whitish-green, stigmas sessile. Fruits 10–20 per umbellule, each with 5 or 6 locules (each 1-seeded), globose-ovoid, 7–8 mm long, 6–7 mm in diameter, turning white (when immature) then maturing to pale pink, tightly clustered at maturity, forming a distinct hemispheric or mound-shaped infructescence.

Notes. *Osmoxylon leidichii* occurs across the limestone islands of Palau on karst and coral substrates and within this range it appears to be common. It has been previously confused with *O. pachyphyllum*, but is distinguished by its 7–9 rhombic leaf lobes, its appressed, flakey stipules, and its inflorescences, which bear many more fruits that are each smaller and more globose. One of the syntypes (*R. Kanehira* 2452) cited in the protologue of *Boerlagiodendron pachyphyllum* belongs to this new species. We are happy to name this species after the Palau resident and naturalist, Ron Leidich, whose generosity enabled the discovery of this species and for his inspirational knowledge and enthusiasm about Palau's natural history.

Specimens examined. **Palau.** Koror State: Ngeremdiu Beach, 6 Jun 2014 (ster.), C. Costion 3708 (US); Ngeremdiu Beach, 6 Jun 2014 (fl.), C. Costion 3709 (BNM); Ngeremdiu Beach, 6 Jun 2014 (fl.), C. Costion 3710 (NY, US); Ngeruktabel Island, 26 Jun 1982 (fr.) Hobdy 1547 (BISH); uninhabited coral island, 14 Aug 1933 (ster.) *R. Kanehira* 2452 (TI, FU); Ngeruktabel Island, 8 Aug 2007 (fr.) M. Balick 4511 (BNM, NY); Ngeruktabel Island, along path from boat landing to German Lighthouse, 07°15'50.3"N; 134°26'45.9"E, 135 m, 9 Nov 2013 (ster.), G.M. Plunkett 2707 (BNM).

***Osmoxylon ngardokense* Costion, sp. nov.**

urn:lsid:ipni.org:names:77151880-1

Fig. 2

Type. **Palau.** Melekeok: Ngardok forest dynamics plot, 07°30'36.97"N, 134°36'28.04"E, 50 m, 17 Jul 2014 (fr.) C. Costion 3721 (holotype: NY; isotype: BNM, US).

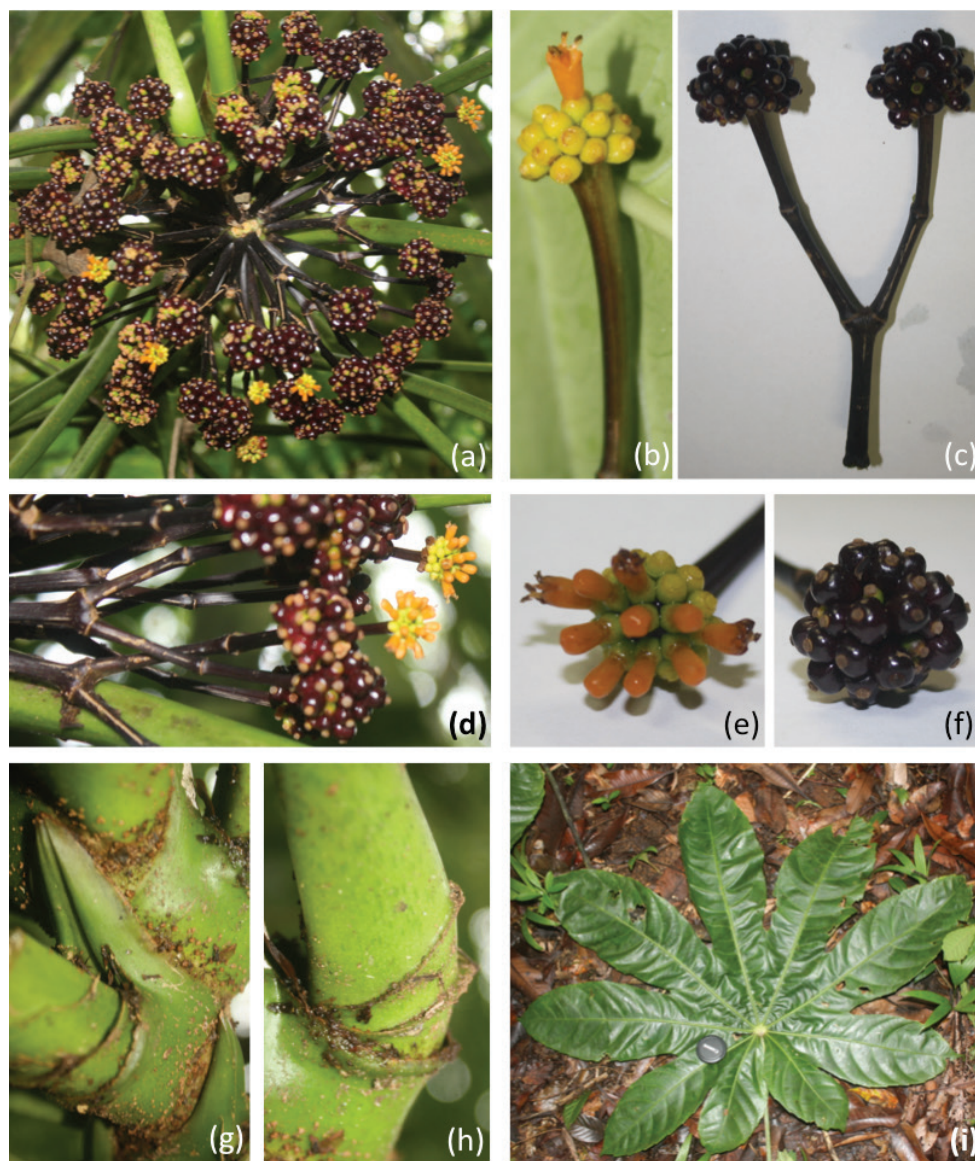


Figure 2. *Osmoxylon ngardokense* **a** compound inflorescence **b** inflorescence **c** inflorescence with mature fruits **d** inflorescences fruiting and flowering **e** flower head up close **f** mature fruits up close **g** petiolar stipule **h** petiole crests **i** leaf.

Description. Small understory tree, 7–10 m tall, unbranched. Leaf blades large with distinct celery smell when crushed, up to 60 cm long and 75 cm wide, with 9–11 lobes; margin weakly serrated, serrations exserted or protruding from margin and spaced far apart, generally 1 per secondary vein or up to one between secondary veins; prominent secondary veins 8–13 per lobe, meeting the mid-rib at a near 90° (perpen-

dicular) angle then curving to a 30–45° angle; petioles up to 92 cm in length; petiolar crests 3, circular, with papery edge and minutely toothed; stipule 3.5–4 cm long, deeply furrowed, slightly appressed to stem and mildly recurved on the axial side, tip not sharp or firm. Inflorescence 20–25 cm in diameter, primary axis bearing 30–40 secondary inflorescence units, secondary axis (from primary axis to where lateral umbellules are attached) c. 3.5 cm long, sterile fruits not seen; lateral peduncles jointed, c. 4–5 cm long, bottom segment 1.2–1.5 cm, top segment 2.5 cm; dark purplish-black in color. Fertile flowers 20–30 per umbellule, with light-green, fused or united, globose to cup-shaped calyx, 2–2.5 mm long; corolla tube bright yellow-orange, 4–5 lobed, 3 mm long, 1.5–2 mm wide; stamens alternate to the petal lobes, partially exserted; ovary inferior, greenish, stigmas sessile. Fruits 30–40 per umbellule, with 5 locules (each 1-seeded), globose, 3–6 mm in diameter, turning dark blackish-crimson; fruiting umbellules globose, 2–2.5 cm in diameter at maturity, spaced apart, not densely packed.

Notes. *Osmoxylon ngardokense* is so far known only from the type locality, with volcanic soil, near Lake Ngardok on Babeldaob, within the Ngardok Nature Reserve, for which the species is named. This species is clearly distinct from the other Palau taxa of *Osmoxylon* by its large 9–11 lobed leaves, large compound inflorescence with inflorescences widely spaced, and dark crimson globose fruits in globose clusters of 30–40.

Specimens examined. Palau. Melekeok State: Ngardok Nature Reserve in Ngardok forest dynamics plot, 21 Jul 2014, 23 Jul 2014, C. Costion 3895 (BNM), C. Costion 3725 (NY).

Osmoxylon truncatum (Kaneh.) Fosberg & Sachet

Fig. 3

Boerlagiodendron truncatum Kaneh., Bot. Mag. Tokyo, 48: 403, fig. 2, 1934.

Osmoxylon oliveri Fosberg & Sachet, Smithsonian Contr. Bot. 45: 16. 1980.

Type. Palau. Ngardmau: near Dudui's homestead, 2 Apr 1966 (fr., fl.), Cheatham 54 (holotype: US!; isotype: NY!, BISH!).

Type. Palau. Aimeliik State: 2 Aug 1933, R. Kanehira 2364 (holotype FU!; isotype: NY!).

Description. Small to medium-sized understory tree, 10–20 m tall, branched. Leaf blades palmately lobed and large, up to 80 cm long and 85 cm wide, glabrous, generally with 11–15 lobes, strongly serrated; serrations protruding from margin, 2 or 3 in between each prominent secondary vein; prominent secondary veins meeting the mid-rib at a sharp 45° angle; petioles up to 1.2 meters long, petiolar crests 3 or 4, circular, ciliate; stipule appressed to stem, shallowly furrowed on top with 1–3 ciliate crests resembling horizontal lines of teeth or wart-like projections; margin of stipule papery and tannish, expanding in towards the center as the stipule matures. Compound inflorescences 20–30 cm in diameter, primary axis bearing 20–40 secondary inflorescence units, secondary axis (from primary axis to where lateral umbels are attached) 3–6 cm long, supporting an umbel of 20–30 dark purple to blackish baccate pseudo-fruits up

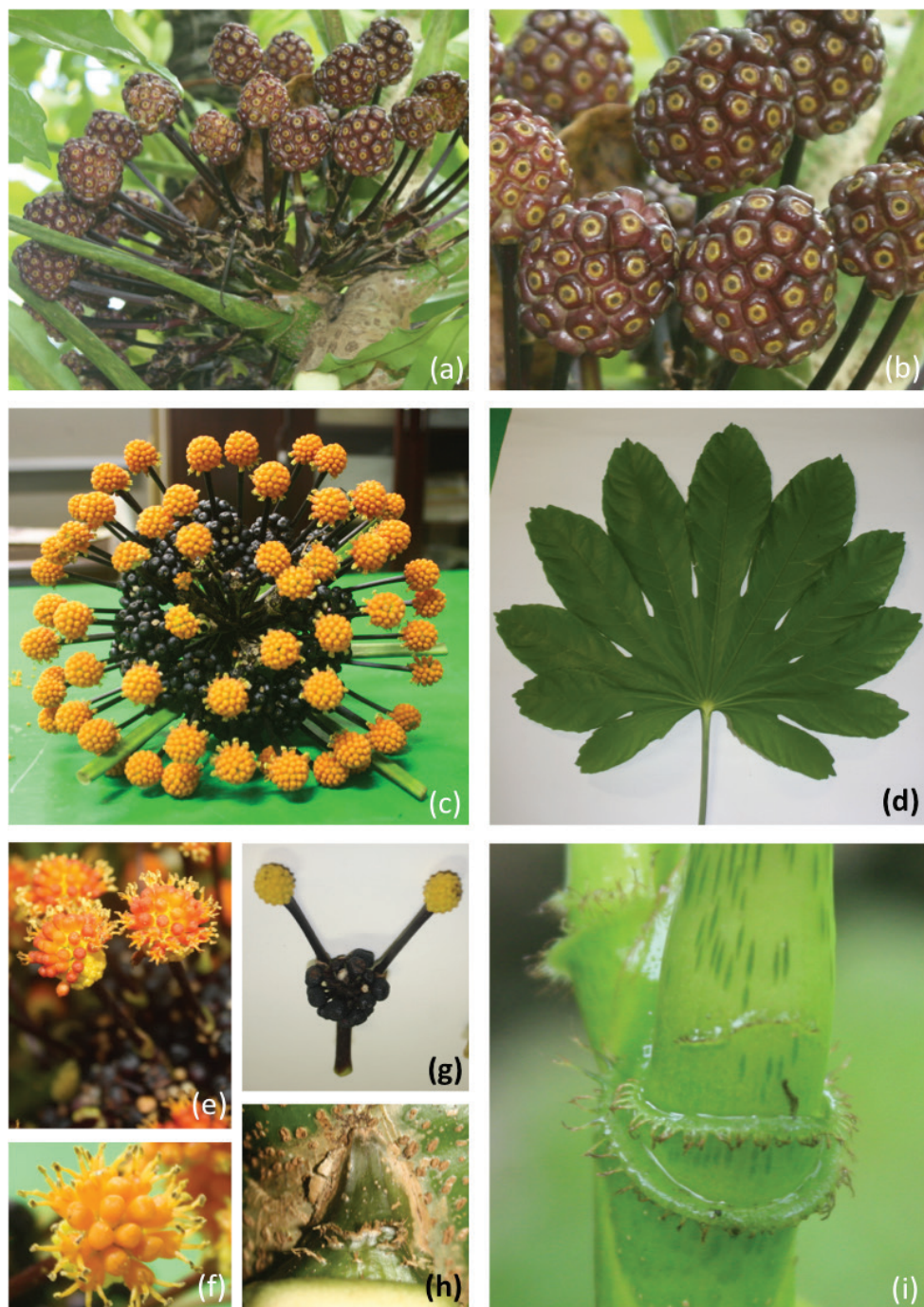


Figure 3. *Osmoxylon truncatum* **a** compound infructescence with mature fruits **b** mature fruits **c** compound inflorescence with un-opened flowers **d** mature leaf **e** one mature inflorescence **f** flower head **g** one fertilized inflorescence, without corollas **h** petiolar stipule **i** petiole crests.

to 1 cm in diameter; peduncles jointed, purple, 5–7 cm long, with bottom segment 2–6 times shorter but becoming longer with maturity. Flowers 45–80 per head with yellow, angular, bright yellow calyx crowning the ovary; corolla tube bright reddish-orange, 5-lobed, 4 mm long; stamens alternate to the petal lobes, strongly exserted; ovary inferior with sessile stigma. Fruits pedicelate, obpyramidal, resembling corn kernels, each c. 1 cm long, 1 cm wide, greenish to white, maturing with a dull purple apex and striations down to the base; fruiting umbellules c. 5 cm long, 4 cm wide, mulberry shaped, with up to 80 fruits densely pressed together.

Notes. *Osmoxylon truncatum* is common in both the limestone and volcanic islands of Palau and is often found in villages near dwellings. The flowers are used for decorations in traditional and modern customs and events. The species is distinguished from the other Palau *Osmoxylon* taxa by its leaves with 11–15 lobes, ciliate crested stipules, and its much larger inflorescences with up to 80 flowers and fruits.

Specimens examined. **Palau.** Aimeliik State: along road to power plant, Dec 2014, Costion 3987–3989, (BNM, US); Airai State: just south of main entrance to airport, 07°21'49.0"N; 134°31'54.1"E, 64 m, 12 Nov 2013 (fl., fr.), G.M. Plunkett 2716 (BNM, NY); Ngetkib, agroforest, 7 Aug 2007 (fr.), M. Balick 4475 (BNM, NY); near airport, 15 Oct 1978 (fl.) Shearard & Spence 89 (BISH); Babeldaob, 1 Nov 1933 (fl.) Herre 71 (BISH); Kaiguru, 15 Apr 1936 (fl.), Takamatsu 1611 (BISH); Koror State: Koror, BNM botanical garden, 9 Mar 2007 (ster.), Kitalong 30907 (BNM); Coral island, Aug 1932, Kanehira 1853 (FU); Aug 1929, Kanehira 129 (FU); BNM botanical garden, 5 Dec 2014, Costion 3980–3986, 3990–4000 (BNM, US); Melekeok State: Aug 1932, Kanehira 2057 (FU); Ngaraard State: tributary of Ngereakl R., 20 Jan 1978 (fr.) J. Canfield 397 (BNM, BISH); Ngarchelong State: west of Pkulrengerealong, 3 Jan 1978 (ster.), J. Canfield 304 (BMM); Ngaremlengui State: upper Ngarmiskan R., 8 Dec 1978 (fr.) J. Canfield 650, 651, (BNM); Ngatpang State: Mechutelngatpang, 5 Aug 2008 (fr.), M. Balick 4594 (BNM, NY); Ngiwal State: along Ngareboku R., 17 Jan 1978 (ster.), J. Canfield 362 (BNM); Aug 1932, Kanehira 2065 (FU), Aug 1932, Kanehira 2066 (FU).

Osmoxylon pachyphyllum (Kaneh.) Fosberg & Sachet

Fig. 4

Boerlagiodendron pachyphyllum Kaneh., Bot. Mag. Tokyo, 48: 401, 1934.

Type. Palau. Aimeliik: 1933 (fr.), R. Kanehira 2301 (lectotype: FU!, here designated; isolectotype: TI!).

Description. Small to medium sized understory, tree 7–15 m tall, sparsely branched. Leaves palmately lobed, variable in size, up to 60 cm long and 65 cm wide (generally smaller), with 5–7 lobes; margins sparsely dentate with serrations exserted from margin, 1 per prominent secondary vein or alternating between veins; prominent secondary veins meeting the mid-rib (near) perpendicular then curving to a 30–45° an-



Figure 4. *Osmoxylong pachyphyllum* **a** compound inflorescence with mature flowers **b** compound inflorescence with immature flowers **c** compound inflorescence with mature fruits **d** two inflorescences with mature fruits **e** mature leaf **f** petiolar stipule and petiole crests.

gle; petiolar crests 1–2, rarely 3, firm with sharp edges, sparsely ciliate; stipules not appressed to stem, strongly recurved, glabrous, tip sharp to the touch. Inflorescence 7–15 cm in diameter, primary axis bearing 12–15 secondary inflorescence units, secondary

axis (from primary axis to where lateral umbellules are attached) c. 2.8 cm long, with c. 30 pinkish-red baccate pseudo-fruits, c. 4 mm in diameter; peduncles jointed, c. 2.6 cm long, top segment shorter, maturing to equal the length of the bottom segment, green. Fertile flowers 10–15, with greenish-yellow, fused calyx crowning the ovary; corolla tube yellowish-orange, 6 lobed, c. 5 mm long; stamens alternate to the petal lobes, strongly exserted; ovary inferior, stigmas sessile. Fruits flat sided, 1.2–1.5 cm long, 0.7–0.8 cm wide, greenish with reddish-dull purple apex and striations down to the base, c. 3–5 per umbellule; fertile fruiting umbellules loosely organized with distinct peduncles, 1.5–3 cm diameter.

Notes. As circumscribed herein, *Osmoxylon pachyphyllum* is known only from volcanic soils on Babeldaob Island. Previous collections of this species from the limestone islands (including a syntype, R. Kanehira 2452) are now referred to the new species *O. leidichii*. In addition to its geography and ecology, *O. pachyphyllum* can easily be distinguished by its 5–7 lobed and weakly serrated leaves, its oblong, large, angled fruits, and its umbellules, which have very few (3–5) fruits, compared to all other species known from Palau. The stipule at the petiole base is also distinctive among the Palauan members of the genus in being strongly recurved, pointing away from the stem, and with a noticeably sharp tip.

Specimens examined. Palau. Aimeliik State: slope of Ngetchum, 28 Dec 2005 (fl.) C. Costion 894 (BNM); Jul 1933, Kanehira 2301 (FU); 30 Jul 1933, Kanehira 2311 (FU); Babeldaob Island, south central Babeldaob, SW of Mt. Yekigoroto, 2 Sep 1965 (fr.), R. Fosberg 47677 (BISH); Babeldaob Island, 17 Apr 1938 (flw), Hatusima 5021 (FU); Babeldaob Island, 18 April 1938, Hatusima 5053 (FU); Melekeok State: Ngardok Nature Reserve in Ngardok forest dynamics plot, Jul 2014 (fr., fl.) C. Costion 3779, 3780, 3781, 3802 (BNM, US); Ngardmau State: 2005 (fr.), C. Costion 90 (BNM); Ngertebechel watershed south of waterfall, 15 Jul 2005 (fl.), C. Costion 449 (BNM); Ngaremlengui State: along trail from Mr. Ha's quarry to Parkia population and waterfall, 07°32'39.6"N; 134°34'07.2"E, 131 m, 5 Nov 2013 (bud, fl., fr.), G.M. Plunkett 2686 (BNM, NY); Ngechesar State: along Iliud ra mesial historic trail, 99 m, 7 Jun 2014 (fr.) C. Costion 3712 (BNM, US), 7 Jun 2014 (fr.) C. Costion 3713 (NY), 7 Jun 2014 (fl.) C. Costion 3714 (NY), 7 Jun 2014 (fr.) C. Costion 3715 (BNM, NY, US), 7 Jun 2014 (fl.) C. Costion 3716 (BNM, US), 7 Jun 2014 (fl.) C. Costion 3717 (US), 7 Jun 2014 (fr.) C. Costion 3719 (NY, US)

Discussion

Vegetative characters

The most useful characters for distinguishing among the species of *Osmoxylon* present in Palau are summarized in Table 1. Of these, leaf size can vary considerably between individual trees within each species. The number of lobes sometimes varies due to slower development of basal lobes. The presence of distinctive veins present at the leaf

Table 1. Diagnostic morphological characters useful for distinguishing the Palau *Osmoxylon* species.

Diagnostic Characters	<i>O. leidichii</i>	<i>O. ngardokense</i>	<i>O. truncatum</i>	<i>O. pachyphyllum</i>
LEAVES				
Mature leaf lobes	7–9	9–11	11–15	5–7
Serrations	Inserted, 1 per secondary vein	Exserted, 1 or 2 per secondary vein	Exserted, 2 or 3 per secondary vein	Exserted, 0 or 1 per secondary vein, sometimes absent
Secondary vein orientation	30–45°angle with midrib	Near 90°angle with midrib	30–45°angle with midrib	Near 90°angle with midrib
Stipule	Appressed to stem, tannish pubescence	Appressed to semi-recurved, glabrous	Appressed to stem, ciliate crests/teeth	Recurved, glabrous, tip sharp
FLOWERS				
Compound umbel dia.	10–15 cm	20–25 cm	20–30 cm	7–15 cm
No. inflor-escences per compound umbel	20–30	30–40	20–40	12–15
No. flowers per head	10–25	20–40	45–80	10–15
Fertile peduncles	c. 3 cm, not distinctly jointed	4–5 cm, jointed, bottom segment shorter maturing to equal top segment	5–7 cm, jointed, bottom segment 2–6 times shorter	c. 2.6 cm, jointed, top segment shorter maturing to equal bottom segment
FRUITS				
No. per head	10–25	20–40	Up to 80	3–5
Head shape	Globose	Globose	Oblong	Umbel
Head size	1.5–2 cm dia.	2–2.5 cm dia.	4–5 cm dia.	1.5–3cm dia.
Fruit size	0.7–0.8 × 0.6–0.7 cm	0.3–0.6 cm	1.0 × 1.0 cm	1.2–1.5 × 0.8 cm
Shape	Globose-ovoid slightly angled	Distinctly globose	obpyramidal (corn kernel)	Oblong, flattened sides
Color	White maturing to pinkish	Shiny dark purple-blackish	White-green maturing to dull purple from apex	Yellow-green with maroon-dull purple striations and apex
Compound inflorescence shape at fruit maturity	Hemispheric	Globose	Globose	Umbel-shaped

base often indicates an undeveloped lobe. We found that the number of lobes can be useful in the field for distinguishing among species if caution is used in inspecting several leaves per tree. Optimally, this information should be recorded as label data for herbarium specimens, but because most specimens do not include such data, leaf-lobe number alone is not sufficient for identifying herbarium specimens, especially given the tendency of collectors to select smaller leaves (often the reduced ones emerging directly under inflorescences) that are easier to press. The leaf-margin serrations can also be useful, particularly the number of teeth per prominent secondary vein. In this regard, *O. leidichii* is very distinct from the three other Palauan species in having teeth occurring in indentations in the margin with the tooth apex not exceeding the margin.

The angle of the junction between the secondary veins and primary veins cannot be used alone, but can help rule out two out of the four Palau species, and the stipule also has diagnostic value. The petiolar crests or rings are sometimes used to distinguish *Osmoxylon* species in other geographical regions. Among the Palauan taxa, the number of petiolar crests can vary within each species, but they have somewhat different margins (e.g., ciliate or nearly entire). These features are sometimes absent or not persistent and are therefore not sufficiently distinct to distinguish the Palau species in the absence of other characters.

Reproductive characters

Diagnostic reproductive characters include the size of the inflorescence, the number of secondary inflorescence units, the number of flowers per head or umbellule, and various features of the peduncles of the fertile heads. The fertile heads or umbellules of three out of the four Palau species have distinctly jointed peduncles, where caducous bracts are present. The peduncles also differ in the proportional lengths of the upper or lower segments (above and below the bracts or bract scars). Bracts tend to subtend each segment of the compound inflorescence but are rarely persistent and thus their morphology does not provide reliable characters. Floral characters are similar among the four species, each having yellow-orange corollas with 4-6 lobes and cup-shaped or globose calyces surrounding the ovary. When present, features of the mature fertile fruits (their size, shape, and color, as well as the number of fruits per umbellule) can be used to distinguish unambiguously among all four Palau species and seem to be the most reliable diagnostic characters. This suggests that fruiting material is particularly important for understanding species limits within the genus and is particularly desirable for recognizing and describing new entities.

Resolving the identity of *O. truncatum*

Osmoxylon truncatum was previously known only from two collections, neither of which contained mature fertile parts (type: R. Kanehira 2364, and R. Kanehira 2303). Thus, resolving its correct identity required considerable effort. All other records attributed to this species were misidentified collections of either *O. oliveri* or *O. pachyphyllum*. The type specimen contains only immature flowers and no fruits are known. Kanehira (1934) noted that this species differs from the other Palauan taxa in having central infertile umbellules borne on peduncles that are longer than those of the lateral, fertile umbellules, and that the inflorescence heads are smaller. These characters, however, are consistent with the immature state of the inflorescence found on the type of *O. oliveri*. Indeed, smaller inflorescences of *O. oliveri* tend to occur in the deeply shaded understory of forests, whereas trees growing in open habitats tend to have larger inflorescences. Kanehira (1934) also distinguished *O. truncatum* based on its having

leaves with a truncate base and 7 lobes. However, truncate leaf bases have also been observed in some specimens of both *O. oliveri* and *O. pachyphyllum*. The number of lobes can be a useful guide for identifying species of *Osmoxylon* in Palau, but is not suitable as a primary feature for delimiting new species without mature flowers and/or fruits, as was done in the case of *O. truncatum*. Young leaves and those directly subtending inflorescences have fewer lobes than the leaves at full maturity, regardless of the species.

To address these uncertainties, we carefully examined the immature inflorescences of the type specimen of *Osmoxylon truncatum* in the Kyushu University herbarium (FU) and collected immature inflorescences of the other species recognized here for comparison. Most convincing in our assessment were recent collections of *O. oliveri*. Careful examination of immature inflorescences from 17 different trees of *O. oliveri* revealed variation in the size and length of inflorescence parts, and the measurements of material ascribed to *O. truncatum* fit within this range. More importantly, one collection (Costion 3985) matches the general appearance of inflorescences on the type of *O. truncatum* (Suppl. material 1).

To pursue this matter further, we traveled to the type locality of *O. truncatum*, Aimeliik on the island of Babeldaob. After observing numerous individuals of *O. oliveri*, we made three new collections (Costion 3987, 3988, and 3989) of this species (See Suppl. material 1), all of which contained leaves on young sprouting branches with 5–7 lobes. Costion 3987 was a mature tree along the roadside that had been pruned. All its branches were re-emergent with many 7-lobed leaves. Notably, leaves in upper or higher branches were up to 10-lobed. Costion 3988 was a sapling with 7-lobed leaves that was clearly a juvenile growing directly underneath a fully fruiting, mature individual of *O. oliveri*. Costion 3989 was notable in that at the base of the trunk, emerging branches contained 5–7-lobed leaves while more mature leaves in the crown of the tree were 11–13-lobed.

Although there are no known mature inflorescence characters for Kanehira's species *O. truncatum*, the immature characters of both the leaves and inflorescences match those of *O. oliveri*. Therefore, we treat these two entities as a single species, *O. truncatum*, which has nomenclatural priority.

Geography

The distribution of the genus *Osmoxylon* is particularly curious, suggesting a pattern of East Malesian bird dispersal. The inflorescence morphology also appears to be perfectly suited for bird pollination. Because the fleshy pseudo-fruits mature as the fertile flowers present pollen, we hypothesize that they may act as a lure to attract birds, who then brush against the fertile flowers of the two lateral peduncles (see also Stone 1962). To date, there have been no published accounts reporting observations on pollination or fruit/seed dispersal in *Osmoxylon*. Locals in Palau report that the Micronesian starling, *Alponis opaca orii*, frequently feeds on the fruits, but these observations do not detail effective pollination nor specify whether the feeding is on the sterile baccate pseudo-

fruits or the fertile fruits. We suggest that birds are involved in both pollination (enticed by the pseudo-fruits) and seed dispersal (through the fertile fruits), but observations are needed to record nectar feeding and visits to *Osmoxylon* inflorescences to feed on the fruits and pseudo-fruits by birds or other potential pollinators. Our description of two new species from areas of Palau that have been frequented by professional plant collectors over nearly a century attests to how little is still known about this fascinating genus of plants with such a unique floral and fruiting morphology. We hope this study inspires further data collection on other aspects of these poorly known species.

Acknowledgements

This work was made possible through the funding of the Institute of Pacific Islands Forestry, US Forest Service. We would like to especially also thank Susan Cordell, Christian Giardina, Julian Dendy, Kevin Mesebeluu, Lori Colin, Misako Mishima at the Kyushu University Museum herbarium, Ron Leidich, Palau Forestry, the Ngardok Nature Reserve, Melekeok State, Ann Kitalong, the Belau National Museum, the Coral Reef Research Foundation of Palau, Michael Balick, and the National Geographic Society.

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Supplementary material I

Supporting evidence for the treatment of *O. oliveri* and *O. truncatum* as one species

Authors: Craig M. Costion, Gregory M. Plunkett

Data type: species images

Explanation note: Photos of flowers taken under microscope. Photos of leaves taken in the field at the type locality of *O. truncatum*.

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A comprehensive checklist of vascular epiphytes of the Atlantic Forest reveals outstanding endemic rates

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Academic editor: *Rejane P. Oliveira* | Received 10 July 2015 | Accepted 14 November 2015 | Published 12 January 2016

Citation: Freitas L, Salino A, Neto LM, Almeida TE, Mortara SR, Stehmann JR, Amorim AM, Guimarães EF, Coelho MN, Zanin A, Forzza RC (2016) A comprehensive checklist of vascular epiphytes of the Atlantic Forest reveals outstanding endemic rates. *PhytoKeys* 58: 65–79. doi: 10.3897/phytokeys.58.5643

Abstract

Knowledge of the geographic distribution of plants is essential to underpin the understanding of global biodiversity patterns. Vascular epiphytes are important components of diversity and functionality of Neotropical forests but, unlike their terrestrial counterparts, they are under-represented in large-scale diversity and biogeographic analyses. This is the case for the Atlantic Forest - one of the most diverse and threatened biomes worldwide. We provide the first comprehensive species list of Atlantic Forest vascular epiphytes; their endemism patterns and threatened species occurrence have also been analyzed. A list with 2,256 species of (hemi-)epiphytes - distributed in 240 genera and 33 families - is presented based on the updated Brazilian Flora Checklist. This represents more than 15% of the total vascular plant richness in the Atlantic Forest. Moreover, 256 species are included on the Brazilian Red List. More than 93% of the overall richness is concentrated in ten families, with 73% represented by Orchidaceae and Bromeliaceae species alone. A total of 78% of epiphytic species are endemic to the Atlantic Forest, in contrast to overall vascular plant endemism in this biome estimated at 57%. Among the non-endemics, 13% of epiphytic species also occur either in the Amazon or in the Cerrado - the other two largest biomes of Brazil - and only 8% are found in two or more Brazilian biomes. This pattern of endemism, in addition to available dated phylogenies of some genera, indicate the dominance of recent radiations of epiphytic groups in the Atlantic Forest, showing that the majority of divergences dating from the Pliocene onwards are similar to those that were recently reported for other Neotropical plants.

Keywords

Angiosperms, canopy, ferns, lycophytes, hotspots, life-forms, monocots, tropical forests

Introduction

Geographic distribution of vascular plant species forms the framework to understand terrestrial diversity patterns, their relationship to environmental and historical factors and the ecological and evolutionary mechanisms underlying these patterns (Currie et al. 2004, Ricklefs 2004, Kreft and Jetz 2007). The Neotropical region harbours more species than any other place on Earth (Gentry 1982). However, the scarcity of distributional data has hampered progress towards developing more general models for the region (Kamino et al. 2012). Vascular epiphytes are known to be an important component of plant diversity in Neotropical forests, although less is understood about their ecology and phytogeography than about their terrestrial counterparts (Kreft et al. 2004). This lack of knowledge of vascular epiphytes stems from logistical constraints associated with the collection of samples (Barker and Pinard 2001, Burns and Zotz 2010). Whether richness and endemism patterns of Neotropical ecosystems are similar for epiphytes and terrestrial plants remains an underexplored question (see Fontoura et al. 2012).

The high abundance of vascular epiphytes constitutes a remarkable characteristic of tropical forests. These plants may exceed 50% of local vascular plant richness in some montane forests (Kelly et al. 2004) and as many as 126 species have been found on a single tree (Schuettepelz and Trapnell 2006, see also Krömer et al. 2005). The importance of epiphytic plants functional role in forest communities cannot be underestimated, as they influence nutrient cycles and provide shelter as well as nesting materials and food for animals (review in Bartels and Chen 2012). They can also enhance diversity, as is the case of the microcosms associated with bromeliad phytotelmata (Richardson 1999). Epiphytes represent 9–10% of the total known vascular flora, comprising between 23,000 and 29,000 species, distributed among 73–84 families (Kress 1986, Gentry and Dodson 1987, Zotz 2013) but most species belong to a few families (e.g., about 80% of the species belong to the Orchidaceae, Araceae, Bromeliaceae, Polypodiaceae and Piperaceae; Gentry and Dodson 1987). Although taxonomic distribution of epiphytism in vascular plants is well established, few studies explicitly address biogeographical aspects of epiphytes (reviewed in Kreft et al. 2004).

The Atlantic Forest, one of the floristic diversity centres in the Neotropics (Gentry 1982, Stehmann et al. 2009) used to be among the largest tropical forests of the Americas, originally covering around 150 million hectares. Unfortunately, only 12% of the original area still remains (Ribeiro et al. 2009). This biome occupies a narrow strip of land along the eastern coast of Brazil, from sea level towards the west, reaching the hinterland mountains (up to 3,000 m) and becoming broader between southeastern and southern Brazil. With a latitudinal range spanning from around 6° to 30°S, it spreads from tropical into subtropical regions, covering 13% of the Brazilian

territory. Around 95% of this vast biome occurs in Brazil, extending only marginally into Argentina, Paraguay and Uruguay (Ribeiro et al. 2009, Stehmann et al. 2009). Altitudinal, latitudinal and longitudinal ranges create highly heterogeneous environmental conditions that lead to highly variable forest composition. While the coastal areas receive abundant rain all year-round, reaching more than 4,000 mm/year, inland forests receive as little as 1,000 mm/year, and this precipitation is distributed according to a seasonal pattern (Câmara 2003). Recent compilations regarding Brazilian floristic diversity recorded more than 16,000 species of vascular plants for the Atlantic Forest, approximately half of them being endemic to this biome (e.g., Stehmann et al. 2009, Forzza et al. 2012, List of Species of the Brazilian Flora 2014). These compilations offer important insights into the significance of the Atlantic Forest for Neotropical diversity and provide a basis for other studies related to biodiversity and conservation.

This paper provides the first comprehensive species list of vascular epiphytes for the Brazilian Atlantic Forest, identifying: (i) taxonomic representativeness, (ii) geographic distribution and endemism, and (iii) occurrence of threatened species among epiphytes of this biome. This study is the first approach to the analysis of epiphyte diversity patterns in the Neotropics involving the mechanisms underlying floristic diversity in tropical forests.

Methods

Raw data for this study were obtained from the database developed by Stehmann et al. (2009). This list includes 14,552 vascular species from different vegetation types within the original extension of the Atlantic Forest, according to Brazilian legislation (Atlantic Forest law, n°. 11,428). Plant habit (hemi-epiphytic or epiphytic) was assigned by consulting labels from the Rio de Janeiro Botanical Garden Herbarium samples (RB, JABOT database, www.jbrj.gov.br), species descriptions in taxonomic literature, and information provided by specialists. Scientific names were updated according to the List of Species of the Brazilian Flora (2014), which listed 15,490 vascular species occurring in Atlantic Forest when last accessed.

All facultative and holoeiphytes, as well as all primary and secondary hemiepiphytes were listed, but accidental and heterotrophic epiphytes were excluded following the concept provided by Benzing (2000). The term epiphyte was used for both holoeiphytic and hemiepiphytic species throughout the text for convenience, with exceptions explicitly mentioned. Geographic distribution patterns were determined for the four major Brazilian biomes (Atlantic Forest, Amazon, Caatinga and Cerrado), based on the same criteria used in The Brazilian Catalogue of Plants and Fungi (Forzza et al. 2010, 2012). Data regarding conservation status were obtained from the Red Book of Brazilian Flora (Martinelli and Moraes 2013). The resulting list was checked for inconsistencies in life-form terminology and geographic distribution, and finally species and family richness and distribution patterns were compared (i.e., endemics to the Atlantic Forest and to Brazil; occurrence in the Atlantic Forest and in one other biome; and widespread species).

Results

Taxonomic diversity

Our compilation recorded 2,256 species of epiphytes distributed in 33 vascular plant families (Suppl. mater. 1). This corresponds to 15% of the vascular flora from the Atlantic Forest (Table 1). Almost one third of fern and lycophyte species from the Atlantic Forest are epiphytes (Table 1).

Representation of vascular epiphytes is highly concentrated in a few families, with the ten richest families accounting for around 93% of epiphyte diversity (Fig. 1). Only nine Atlantic Forest families (five angiosperms and four fern families) are represented by only one or two epiphytic species (Appendix). Orchidaceae and Bromeliaceae comprised the richest families with almost 73% of vascular epiphyte species, while Polypodiaceae alone comprises more than 40% of fern and lycophyte epiphytic species (Fig. 2).

Table 1. Number of vascular taxa for the Brazilian Atlantic Forest. Compiled from the List of Species of the Brazilian Flora (2014).

	Taxonomic group	Families	Genera	Species
All life-Forms	Angiosperms	211	1,975	14,638
	Ferns and lycophytes	36	127	852
	Total - vascular plants	247	2,102	15,490
(Hemi-) Epiphytes	Angiosperms	22	197	2,013
	Ferns and lycophytes	11	43	243
	Total - vascular plants (epiphytes/all life-forms)	33 (13.4%)	240 (11.4%)	2,256 (15.4%)

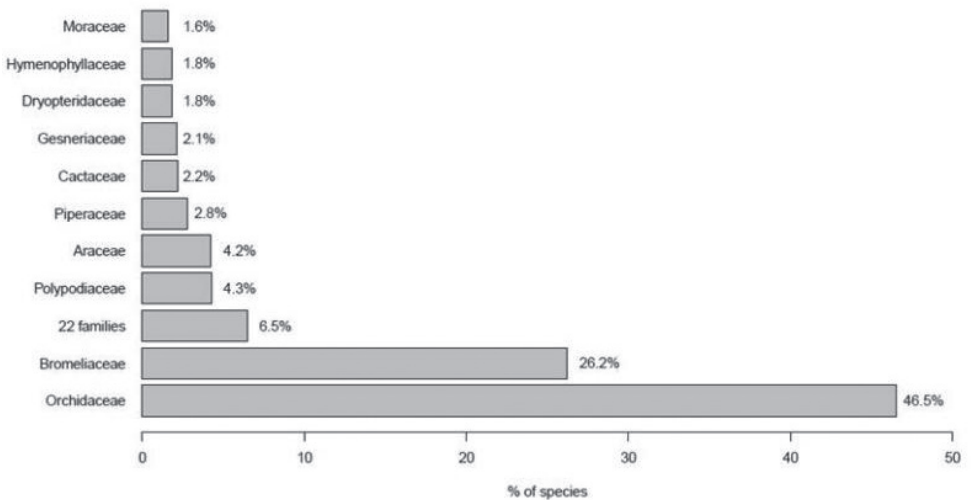


Figure 1. Family representativeness of Atlantic Forest vascular epiphyte species.

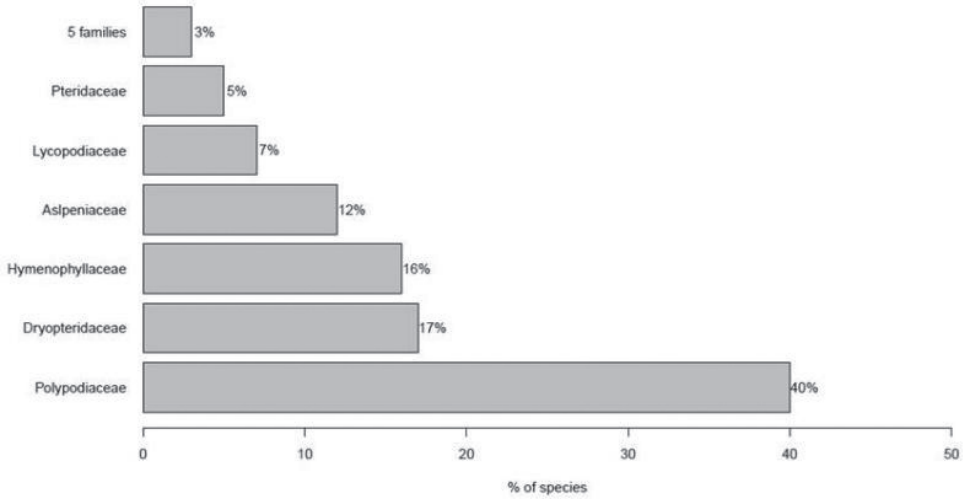


Figure 2. Family representativeness of Atlantic Forest fern and lycophyte epiphyte species.

Table 2. Distribution patterns of vascular (hemi-)epiphytes for Atlantic Forest along the four main Brazilian biomes, and the number of endangered species.

	Number and percentage of species		
	Angiosperms	Ferns and lycophytes	Vascular flora
Restricted to Atlantic Forest	1,595 (79.2%)	146 (60.1%)	1,741 (77.2%)
Atlantic Forest + Amazonia	110 (5.5%)	42 (17.3%)	152 (6.7%)
Atlantic Forest + Cerrado	134 (6.7%)	20 (8.2%)	154 (6.8%)
Atlantic Forest + Caatinga	31 (1.5%)	0	31 (1.4%)
Wide (3 or more biomes)	143 (7.1%)	35 (14.4%)	178 (7.9%)
Endangered species	237 (11.8%)	19 (7.9%)	256 (11.3%)

Geographic distribution and endemism

About three out of four vascular epiphytic species from the Atlantic Forest are endemic to this biome (Table 2), including 21 genera, most of them belonging to Orchidaceae (11) and Bromeliaceae (5). In terms of overall endemism, 78% of the vascular epiphytes of the Atlantic Forest (1,761 species) are endemic to Brazil. Less than 8% of the Atlantic Forest epiphytes are widely distributed (i.e., occur in three or four Brazilian biomes). The remaining 13.5% are species that occur either in the Amazon or Cerrado in addition to the Atlantic Forest (Table 2). Atlantic Forest vascular epiphytes are unequally distributed among angiosperms and ferns and lycophytes, with 60% of the species belonging to the latter group being restricted to the Atlantic Forest, while more than 14% are widely distributed. Moreover, disjunct distribution between Atlantic Forest and the Amazon is higher among ferns and lycophytes (Table 2).

Discussion

Diversity and distributions

Very high levels of vascular epiphytic species richness and endemism were found for the Atlantic Forest, with the vast majority of species being restricted to a small number of plant families. Taxonomic representation of vascular epiphytes for the Atlantic Forest is similar to that found for other tropical forests (Johansson 1989, Wallace 1989, Küper et al. 2004, Obermüller et al. 2014). Moreover, this concentration of epiphytic species in a small number of families in this biome is consistent with worldwide estimates. Orchidaceae, Bromeliaceae, Polypodiaceae and Araceae have had the most success in colonizing the canopy, as they account for 80% of global vascular epiphyte diversity (Kress 1986, Benzing 1990). In fact, the association of epiphytism with high rates of diversification was demonstrated taking into account phylogeny at various levels in both the Bromeliaceae and the Orchidaceae (Givnish et al. 2014, 2015). However, despite expressive species concentration into a few families, others also contribute to the diversity of epiphytic species, and there are a total of 33 families with at least one epiphytic species in the Atlantic Forest. Vascular epiphytes are distributed among 73–84 families worldwide (Kress 1986, Gentry and Dodson 1987, Zotz 2013), supporting the classic idea that epiphytism has evolved many times and in different plant groups (Lüttge 2008).

The high number of species and endemism rate of epiphytes found in the Brazilian Atlantic Forest follows the trend for this biome, one of the leading world hotspots for many groups of organisms including vascular plants (Myers et al. 2000). High diversity and endemism in the Atlantic Forest is frequently associated with high topographic complexity, abundant precipitation, and latitudinal range, favouring an increased variety of habitats (Gentry 1982, Werneck et al. 2011). Two divergent bioclimatic domains have been recognized within the Atlantic Forest, and endemism patterns of vertebrates have been associated with different climate features during the Pleistocene (Carnaval et al. 2014). The existence of areas with relative climatic stability (*refugia*) is at the center of the explanation for the phytogeographic endemism towards the north of the biome, while areas with climatic heterogeneity appear to be associated with the endemism in the south Atlantic Forest. In Myrtaceae, a representative group of trees in the Atlantic Forest, lower extinction rates were found to be associated with those refugium areas, while higher speciation rates were found in southern, unstable areas (Staggemeier et al. 2015). As epiphytes are intrinsically associated with forests, we can expect that similar patterns should be found in typical epiphytic lineages of the Atlantic Forest. In an attempt to answer this question, Fontoura et al. (2012) have found that species similarity among assemblages of epiphyte bromeliads was divided into one block of south–southeastern localities, and a second block of northeastern–southeastern localities, resembling the distribution of phorophyte species.

Nevertheless, a recurrent question regarding the value of focusing on biodiversity hotspots revolves around the conflicting results that often arise when comparing dif-

ferent groups (Prendergast et al. 1993, Kohlmann et al. 2010, Crain and Tremblay 2014). In the present case, 77% of the epiphytic vascular flora endemic to the Atlantic Forest (roughly 80% for angiosperms) contrasts with 57% of the overall vascular flora endemism and with around 60% of endemic tree species found for this biome (Forzza et al. 2010, List of Species of the Brazilian Flora 2014). Moreover, so far vascular epiphyte endemism is the highest registered for any organism group from the Atlantic Forest. This is more, for instance, than the ca. 60% found for amphibians and roughly 30% for mammals (Myers et al. 2000). Epiphytes are very peculiar organisms in terms of their environmental requirements, and three main factors (light, water, and mineral nutrients) limit epiphytic life (Lüttge 2008). Among them, water availability is considered to be the major constraint for epiphytes (Zotz and Hietz 2001), and this can be observed in the Atlantic Forest, where a drastic reduction in species richness and epiphyte abundance has occurred in the drier and more seasonal semi-deciduous forests that occur in the southwestern portion of the biome (Forzza et al. 2014). Accordingly, epiphytes are more abundant where precipitation and air moisture are high, such as in montane rainforests and upper cloud forests (Freiberg and Freiberg 2000).

This high rate of epiphytic endemism in the Atlantic Forest is reinforced by the contiguity of the xeric Caatinga biome that harbours few epiphytic species and may act as a barrier to biotic exchanges between the Atlantic Forest and the rainforest in the Amazonia (Prado and Gibbs 1993). Less than 7% of the epiphytic species (5.5% for angiosperms) are shared between these two biomes. Thus, even the gallery forest expansion that occurred during the Quaternary wet periods (Wang et al. 2004) does not seem to have been highly effective in enabling epiphyte flora exchange. This is the case for some Episcieae-Gesneriaceae clades (*Codonanthe* (Mart.) Hanst. and *Nematanthus* Schrad. lineages) that are absent in the Amazon, Cerrado and Caatinga, suggesting that the spread of a more open vegetation along a dry corridor separating the Atlantic Forest from the Amazon has been an efficient barrier to the dispersal of these groups from the early Miocene to the present day (Perrett et al. 2013). It also seems to have occurred among epiphytic cacti of the monophyletic tribe Rhipsalideae (genera *Lepismium* Pfeiff., *Rhipsalis* Gaertn., *Hattoria* Britton & Rose and *Schlumbergera* Lem.), mostly endemic to the Atlantic Forest (Calvente et al. 2011, Moreno et al. 2015). However some *Lepismium* species have disjunct distribution between the Atlantic Forest and the yungas forest of the eastern Andes, and *Rhipsalis baccifera* (J.M.Muell.) Stearn is the only cactus with an inter-continental distribution (Moreno et al. 2015). Nevertheless, the surrounding drier and/or more seasonal biomes of the Atlantic Forest may not represent such strong barriers for the dispersal of secondary hemi-epiphytes, which are relatively less dependent on air-humidity, at least in their initial seedling establishment stages. For instance, several Atlantic Forest aroid species of the *Philodendron* Schott subg. *Philodendron* lineage that probably diverged during the Latest Miocene/Pliocene are widely distributed, also occurring in the Amazon, Caatinga, and Cerrado (Oliveira 2014). In addition, the diversification of the *P.* subg. *Meconostigma* Schott lineage into the Cerrado biome occurred during the Late Pliocene from Atlantic Forest ancestors (Oliveira 2014).

The historical discussion on geotemporal trajectories of plant diversification in Neotropical biomes has focused on two alternative models: the museum hypothesis, highlighting an ancient history of steady accumulation of diversity, and the cradle model, favouring more recent diversification and high speciation rates (reviewed in Hughes et al. 2013). More recent models and empirical evidence from dated phylogenetic trees combine episodes of rapid and slower diversification for Neotropical plants (see Linder 2008, Antonelli and Sanmartín 2011). There is very little fossil record of epiphytism and classic studies suggested that this habit might have developed fairly recently among vascular plants, with most diversification occurring during the Pliocene-Pleistocene (Benzing 1990, Lüttge 2006). Particularly, in the case of Orchidaceae, recent evidence based on broad-scale phylogeny indicates that epiphytism in the family appears to have evolved once at the base of the upper epidendroids (by far the most representative group of epiphyte orchids) no later than 35 Mya, with most diversification of subtribes from the Miocene on (Givnish et al. 2015). Among Bromeliaceae almost all cases of epiphytism can be traced to two origins: the first occurred at the base of Tillandsioideae, ca. 16.9–15.2 Mya, with dispersal from the Guayana Shield into the Andes, Central America, and/or the northern littoral of South America or Caribbean while the second one occurred more recently in the Late Miocene (ca. 5.9 Mya) in the Atlantic Forest, in the clade including tank bromelioids (Givnish et al. 2014).

The very high endemism rates found for Atlantic Forest epiphytes, in particular for predominantly holoepiphytic groups of angiosperms are in accordance with the idea of predominant recent diversification. This is the case of Bromeliaceae native to the Atlantic Forest, which rates of net diversification are especially high in the bromelioid tank epiphyte clade (1.11 and 1.05 Mya for stem and crown rates, respectively) and the core tillandsioids (i.e., Tillandsioideae minus *Catopsis* Griseb. and *Glomeropitcairnia* Mez; 0.47 and 0.67 Mya) (Givnish et al. 2014). Another example of this is a major clade of the Gesneriaceae tribe Episcieae mentioned above, composed of epiphytic genera *Codonanthe* and *Nematanthus* that are restricted to the Atlantic Forest. Most species in this clade have diverged from the Pliocene onwards (Perrett et al. 2013), coinciding with species of two subgenera of *Philodendron* Schott, *P.* subg. *Meconostigma* and *P.* subg. *Philodendron* (Oliveira 2014) and species of *Rhipsalis*, *Hatiora* and *Schlumbergera* (Cactaceae, tribe Rhipsalideae) (Arakaki et al. 2011, Moreno et al. 2015). Further, more refined studies which trace dated phylogenies at low taxonomic levels and relate determinants of net diversification, key innovations and invasion of specific ecological zones (e.g., Givnish et al. 2014) are necessary to test hypotheses of recent *in situ* diversification predominance of clades belonging to the major epiphytic angiosperm groups in the Atlantic Forest.

The Atlantic Forest holds the highest richness of fern and lycophyte species in Brazil (Prado and Sylvestre 2010), and the biome was defined by Tryon (1972) as one of the primary centres of Neotropical richness and endemism for non-flowering vascular plants. Specific endemism in ferns and lycophytes is known to be less expressive than endemism in flowering plants (Smith 1972). Propagules of these plants are light, wind-dispersed spores that can easily cross geographic barriers (Tryon 1972).

Environmental conditions are, therefore, main features determining geographic ranges in fern and lycophyte species (Page 1979). This is evident in the distribution patterns found within the Atlantic Forest: ferns and lycophytes have more widespread species (species occurring in three or more biomes) than angiosperms. In contrast to the latter, fern and lycophyte species are more likely to occur in forest environments, such as the Atlantic Forest and the Amazon rather than in open, savannic habitats such as Cerrado and xeric Caatinga habitats.

Conservation matters

Currently there are 78 fern and lycophyte species listed as threatened in Brazil (Martinelli and Moraes 2013), and, amongst these, 25% of them are Atlantic Forest epiphytes. Of these endangered species, eight (*Alansmia senilis* (Fée) Moguel & M.Kessler, *Ceradenia capillaris* (Desv.) L.E.Bishop, *Phlegmariurus aqualupianus* (Spring) B.Øllg., *P. mollicomus* (Spring) B.Øllg., *P. taxifolius* (Sw.) Á.Löve & D.Löve, *Stenogrammitis limula* (Christ) Labiak, *Terpsichore semihirsuta* (Klotzsch) A.R.Sm. and *T. taxifolia* (L.) A.R.Sm.) are not endemic to Brasil, presenting disjunct distribution between the Atlantic Forest and the Andes or with Mesoamerica. Considering the other 11 species, a single one, *Phlegmarius martii* (Wawra) B.Øllg., is not endemic to the Brazilian Atlantic Forest. Among epiphyte angiosperms, only 13 out of the 237 threatened species are not endemic to Brazil, as well as 20 species that are not endemic to the Atlantic Forest. All such endangered species have either a small area of occupancy or a small extent of occurrence, and/or are subject to threats due to habitat suppression/ecosystem degradation (see Martinelli and Moraes 2013). Habitat suppression resulting from human impact on vegetation plays an important role in epiphytic communities, as changes in moisture, irradiation and nutrient availability may limit survival and population dynamics of epiphytes (Hietz 1999, Werner et al. 2011). Less-structured secondary vegetation may not offer a similar range of microsites and the diversity of disturbances in space and time that are found in well established forests, and thus, they may be unsuitable for the establishment and survival of certain epiphytic species (Hietz 1999). For instance, mortality of vascular epiphytes was substantially increased on remnant trees in fragmented areas (72% over 3 years) relative to undisturbed forest (11%) in montane southern Ecuador (Werner 2011). Moreover, gradual changes in species richness and abundance of vascular epiphytes were detected from edge to inward at mixed ombrophilous ("Araucaria) Atlantic Forest, reflecting the gradients of light intensity, humidity and other environmental factors after habitat fragmentation (Bianchi and Kersten 2014).

Vascular epiphytes in the Atlantic Forest are possibly more prone to projected effects of global climate change in their area of occurrence, specifically with increased mean temperatures, and higher frequency of drastic events such as long dry periods (Marengo 2007). Such effects may affect air humidity levels required by vascular epiphytes to survive and the integrity of the vertical microclimatic gradient that is crucial

for the maintenance of epiphyte diversity in forests, mainly in those under moderately seasonal climates (Werner et al. 2011), which predominate in the Atlantic Forest. In short, as pointed out by Prendergast et al. (1993), many hotspots are not effective conservation surrogates for rare or restricted species. Therefore, specific conservation actions are needed to ensure the welfare of this peculiar group of plants, in particular for obligate and preferential holoepiphytes.

Conclusion

Vascular epiphytes are a characteristic feature of Neotropical forests, however, our understanding on biogeographical and floristic relationships of epiphytes as well as of the mechanisms that structure epiphyte communities are still rather poor (Kreft et al. 2004 Wagner et al. 2015). As in the majority of Neotropical forest sites (see Kreft et al. 2004), present knowledge on diversity, phytogeography and the community ecology of the Atlantic Forest is mainly based on studies of tree species (e.g., Oliveira-Filho and Fontes 2000, Santos et al. 2010, Eisenlohr et al. 2013). Trees represent about 22% of angiosperm species of the Atlantic Forest (List of Species of the Brazilian Flora 2014), which means that the vascular epiphytes have an equivalent specific diversity (roughly 15%) of the trees found in this biome. Moreover, the high occurrence of endemisms, roughly 77%, is an outstanding feature among vascular epiphytes of the Atlantic Forest, which harbours roughly 7.5 to 10% of the total known vascular epiphytic flora worldwide. These general patterns should be viewed as starting points for further studies focusing on processes and mechanisms to better understand the role of the epiphytes in the dynamics of communities of the Atlantic Forest, as well as the evolution of the most representative groups of Neotropical epiphytes. For instance, studies contrasting the geographic distribution and diversity patterns of epiphytes and trees within the biome, dated phylogenies of those epiphytic clades highly distributed in the biome, and studies on diversification rates, key innovations and functional traits of epiphytes in the assembly of communities are fundamental for answering these questions.

Acknowledgements

This paper results from activities of the Atlantic Forest Epiphytes' Network, an initiative sponsored by the Coordination for the Improvement of Higher Education Personnel (CAPES-PNADB, Brazil). A.M.A., A.S., J.R.S., L.F., and R.C.F. acknowledge the National Counsel of Technological and Scientific Development (CNPQ, Brazil) for their productivity scholarships. We also thank Daniela Zappi and Andrew Smith for the English revision; Jomar Gomes Jardim, Eric de Camargo Smidt and an anonymous reviewer for their constructive comments.

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Supplementary material I

Species list of vascular (hemi-)epiphytes of Brazilian Atlantic Forest

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Data type: species list.

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On the identity of Blanco's *Cissus frutescens* and its correct name in *Melicope* (Rutaceae) with neotypification of *Cissus arborea* Blanco

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Academic editor: P. Acevedo-Rodríguez | Received 6 August 2015 | Accepted 8 December 2015 | Published 12 January 2016

Citation: Appelhans MS, Wen J (2016) On the identity of Blanco's *Cissus frutescens* and its correct name in *Melicope* (Rutaceae) with neotypification of *Cissus arborea* Blanco. PhytoKeys 58: 81–85. doi: 10.3897/phytokeys.58.5847

Abstract

The names *Cissus frutescens* and *C. arborea* have a long history of confusion. *Cissus frutescens* Blanco belongs to the genus *Melicope* (Rutaceae) and we herein correct a nomenclatural mistake made by T.G. Hartley in the revision of *Melicope*. The name *Melicope confusa* (Merr.) P.S. Liu was accepted for this taxon by Hartley. However, *Cissus frutescens* Blanco represents the earliest name for this entity and a new combination, *Melicope frutescens* (Blanco) Appelhans & J. Wen is herein proposed. Neotypification of *Cissus arborea* Blanco is also provided.

Keywords

Blanco, *Cissus*, *Melicope confusa*, *Melicope frutescens*, Nomenclature, Philippines, Rutaceae, Vitaceae

Introduction

The name *Cissus frutescens* Blanco was published in 1837 in the first edition of Francisco Manuel Blanco's *Flora de Filipinas* (Blanco 1837). The description in Spanish was relatively short and did not cite any collection. Blanco's second edition of this work was published in 1845 shortly after his death and included several name changes without comments or reference to the first edition (Merrill 1905). Among these names

is *Cissus frutescens*, which was changed to *Cissus arborea* Blanco, but the treatment of the taxon remained identical to that in the first edition (Blanco 1845).

After Blanco's death, an addendum to the Flora de Filipinas was written by Fernandez-Villar, who considered *Cissus frutescens*/*C. arborea* conspecific with *Evodia roxburghiana* (Cham.) Benth. [*Evodia* = *Euodia*¹, Rutaceae] (Fernandez-Villar, 1877–1883). *Euodia roxburghiana* is currently known as *Melicope lunu-ankenda* (Gaertn.) T.G.Hartley, and interestingly, only a single specimen of this widespread species was cited from the Philippines in the latest revision of *Melicope* and *Euodia* (Hartley, 2001), suggesting that it might be rare in the Philippines. This was highlighted by Merrill, who stated that the species was “not definitely known from the Philippines” (Merrill 1918: 198).

In 1918 Merrill also treated *Cissus frutescens*/*C. arborea* as conspecific with *E. glabra* Blume, noting that “Blanco's descriptions were very indefinite, and the species Blanco described might with equal propriety be reduced to almost any trifoliolate species of *Evodia* with glabrous leaves” (Merrill 1918: 198). In 1918, Merrill mentioned a collection of *Cissus frutescens* that he collected in the vicinity of Blanco's locality for this species (Merrill, *Species Blancoanae* No. 904, Fig. 1). Merrill considered this collection an “illustrative specimen” with duplicates deposited at A, GH, K, L, NSW, NY, P, US and W. In 1922, Merrill published the new species *Euodia confusa* Merr. where Merrill 904 was listed along with many other specimens. Liu (1962) transferred *Euodia confusa* to *Melicope*, a decision which is in agreement with recent revisionary (Hartley and Stone 1989; Hartley 2001) and molecular phylogenetic studies (Appelhans et al. 2014a, b) where a total of seven species, restricted to New Guinea, northern Australia and several Pacific island groups are recognized in *Euodia*. All species of *Euodia* from the Philippines have been transferred to *Melicope* (Hartley and Stone 1989; Hartley 2001).

The latest revision of *Melicope* (Hartley 2001) included the lectotypification and the neotypification of the names *Melicope confusa* and *Cissus frutescens*, respectively. Hartley (2001) reported that the type of *Euodia confusa* (Ramos 15055, PNH) was lost and therefore he chose Borden 3045 (NY) among the paratypes, as its lectotype. He also designated Merrill 904 as the neotype of *Cissus frutescens*, which he placed as a synonym of *Melicope confusa* (Hartley 2001). Merrill 904 is the “illustrative specimen” that Merrill provided for Blanco's names and which was listed in the protologue of *Euodia confusa* (Merrill 1922).

Until the neotypification of *Cissus frutescens* (Hartley 2001), the status of Blanco's names was unclear. Blanco's species descriptions were not detailed enough to differentiate among several species of *Euodia*/*Melicope*, and his collections were lost. However, by assigning a neotype to *Cissus frutescens*, Hartley (2001) definitely associated the specimen Merrill 904 to this taxon name. By the principle of nomenclatural priority the species epithet *frutescens* must be used for the entity of *Melicope confusa*, as *M. confusa* represents a synonym of *Cissus frutescens*. The epithet *frutescens* is not pre-empted in *Melicope*.

¹ Fernandez-Villar used the old spelling *Evodia*, whereas the conserved spelling is *Euodia*

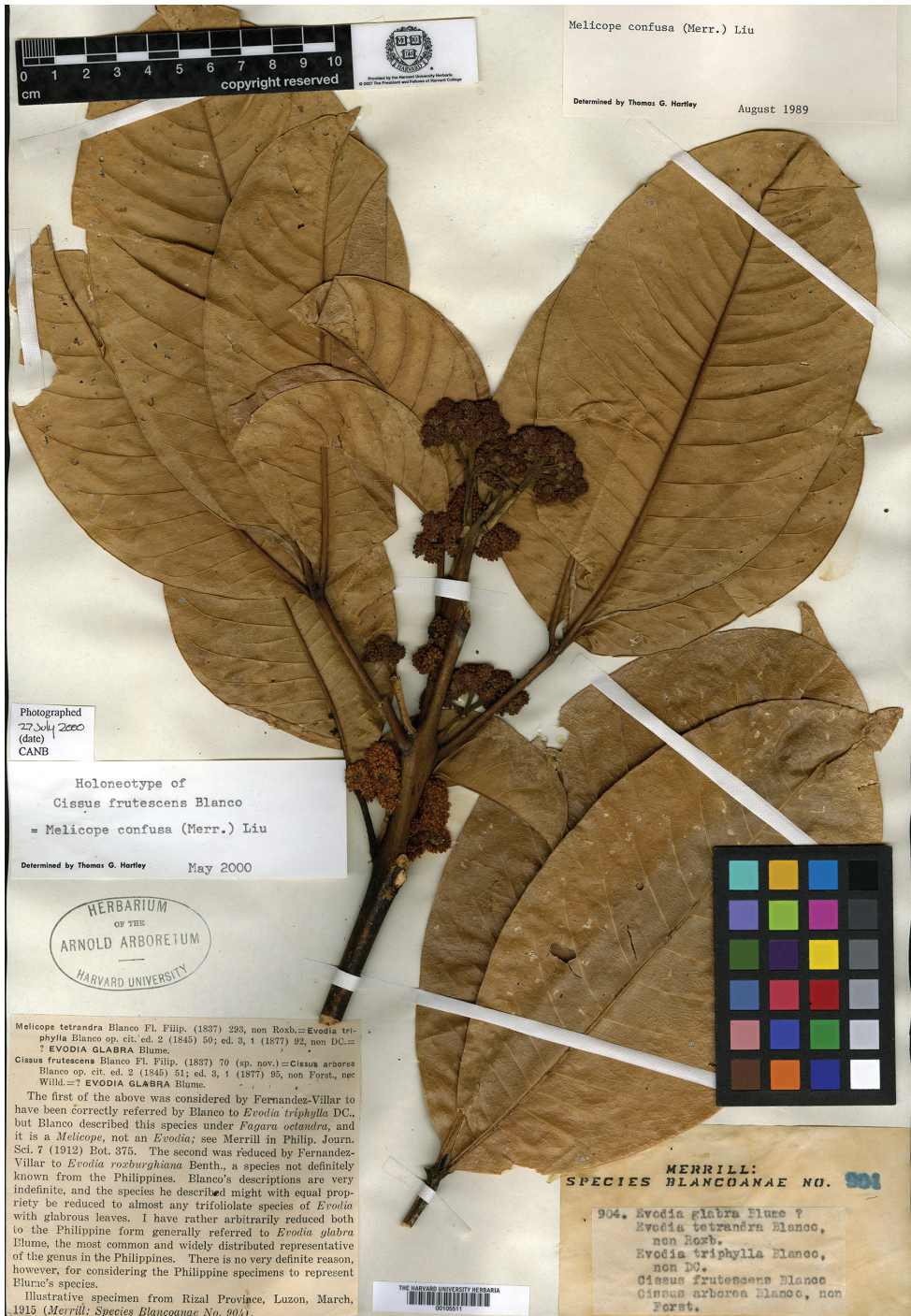


Figure 1. The neotype of *Melicope frutescens* (Blanco) Appelhans & J. Wen (A).

Three other authors used the name *Cissus arborea*. *Cissus arborea* Forssk. (Forsskål 1775) is a synonym of *Salvadora persica* L. (Salvadoraceae; Roemer and Schultes 1818); *C. arborea* Willd. ex Roem. & Schult. is a synonym of *Ardisia guianensis* (Aubl.) Mez. (Mez 1901); and *C. arborea* (L.) Des Moul. is a synonym of *Nekemias arborea* (L.) J.Wen & Boggan (Wen et al. 2014), so the Des Moulins' taxon remains the only *Cissus arborea* that actually represents a Vitaceae species.

Taxonomic treatment

***Melicope frutescens* (Blanco) Appelhans & J.Wen, comb. nov.**

urn:lsid:ipni.org:names:77151881-1

Basionym. *Cissus frutescens* Blanco, Flora de Filipinas, ed. 1: 70. 1837. **Type:** Philippines. Luzon: Rizal, Mar 1915, *Merrill: Species Blancoanae No. 904* (neotype: A!, designated by Hartley 2001, p. 220; isoneotypes: GH!, K, L, NSW, NY!, P!, US!, W).

Cissus arborea Blanco, nom. illeg., Flora de Filipinas, ed. 2: 51. 1845 (non Forssk., 1775). **Type:** Philippines. Luzon: Rizal, Mar 1915, *Merrill: Species Blancoanae No. 904* (neotype: A!, designated here; isoneotypes: GH!, K, L, NSW, NY!, P!, US!, W).

Euodia confusa Merr., Philipp. J. Sci. 20: 391. 1922. *Melicope confusa* (Merr.) P.S. Liu, III. Native Introd. Lign. Pl. Taiwan 2: 876. 1962. **Type:** Philippines. Luzon: Bataan, *Borden FB 3045* (lectotype: NY!, designated by Hartley, 2001, p. 220; isolecotypes: BO, SING, US!).

In addition to its distribution in the Philippines, *Melicope frutescens* is known to occur in Borneo, Sulawesi and the Moluccas. It typically grows in the lowlands but reached elevations of up to 1800 m in the Philippines. The species occurs in primary, secondary, and disturbed rainforests.

Acknowledgements

We thank Sue Lutz for her assistance with obtaining relevant publications, the curators of A for providing a high-resolution image of the specimen *Merrill 904*, Warren Wagner, Larry Dorr and John Boggan for their suggestions, and Pedro Acevedo for his detailed edits of the manuscript. We acknowledge support by the Open Access Publication Funds of Göttingen University.

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Encyclia inopinata (Orchidaceae, Laeliinae) a new species from Mexico

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Academic editor: L. Peruzzi | Received 5 September 2015 | Accepted 10 December 2015 | Published 12 January 2016

Citation: Leopardi-Verde CL, Carnevali G, Romero-González GA (2016) *Encyclia inopinata* (Orchidaceae, Laeliinae) a new species from Mexico. PhytoKeys 58: 87–95. doi: 10.3897/phytokeys.58.6479

Abstract

A new species of *Encyclia* from Mexico, *E. inopinata*, is described and illustrated. This species is similar to *E. diota* but it can be distinguished by its usually more robust plants with 2–3 leaves per pseudobulb and its flowers with longer and narrower sepals ($1.8 \pm 0.1 \times 0.63 \pm 0.03$ cm in *E. inopinata* versus $1.48 \pm 0.14 \times 0.65 \pm 0.06$ cm in *E. diota*) and petals ($1.7 \pm 0.05 \times 0.59 \pm 0.05$ cm in *E. inopinata* vs. $1.36 \pm 0.19 \times 0.81 \pm 0.13$ cm in *E. diota*), and the labellum with narrower lateral lobes (0.18 ± 0.02 cm in *E. inopinata* vs. 0.41 ± 0.10 cm in *E. diota*). Other characters that differentiate these two species are the coriaceous sepals, pink callus, and white anther of *Encyclia inopinata* (versus fleshy-leathery sepals, white callus, and yellow anther of *E. diota*). The new species can be found in deciduous forests along the Pacific slope of Oaxaca state, near of the border with Guerrero state, at about 1200 m. It blooms between March and July.

Resumen

Una nueva especie de *Encyclia* de México, *E. inopinata*, es descrita e ilustrada. Esta especie es similar a *E. diota*, pero puede distinguirse por sus plantas usualmente más robustas con 2–3 hojas por pseudobulbo y sus flores con sépalos y pétalos más largos y angostos (sépalos: $1.8 \pm 0.1 \times 0.63 \pm 0.03$ cm en *E. inopinata* versus $1.48 \pm 0.14 \times 0.65 \pm 0.06$ cm en *E. diota*; pétalos: 1.7 ± 0.05 cm de largo en *E. inopinata* vs 1.36 ± 0.19 cm en *E. diota*), el labelo tiene lóbulos laterales más angostos (0.18 ± 0.02 cm en *E. inopinata* vs. 0.41 ± 0.10 cm en *E. diota*). Otros caracteres que distinguen a las dos especies son los sépalos coriáceos, callo rosa y antera blanca de *E. inopinata* (versus los sépalos carnoso-coriáceos, callo blanco y antera amarilla de *E. diota*). La nueva especie se encuentra en un bosque deciduo del estado de Oaxaca, en la Vertiente del Pacífico, cerca de los límites con el estado de Guerrero, a 1200 m. Florece entre marzo y julio.

Keywords

Encyclia diota, *Encyclia insidiosa*, Pacific slope, Oaxaca

Introduction

Encyclia is a Neotropical genus ranging from Florida in the southern United States of America south to the Salta province in northern Argentina; the distribution includes both the continental areas and the West Indies. Species of the genus are usually found in seasonally dry ecosystems below 1200 m, although some can be found at altitudes of up to 2500 m (van den Berg and Carnevali 2005). According to preliminary phylogenetic analyses, the *Encyclia diota* complex has at least three species, and is morphologically characterized by pyriform pseudobulbs, linear-oblong, relatively wide, and coriaceous leaves, a fractiflex inflorescence with loosely arranged, relatively large, leathery to fleshy-leathery showy flowers, a smooth pedicellate ovary; the sepals and petals are of variable colors, from bronze or ocher to dark chocolate; the labellum is conspicuously trilobulate, the lateral lobes are patent at the apical half or only slightly recurved distally; the callus is glabrous and the column is straight. One of the most distinctive characters of this species complex is the yellow labellum with crimson to reddish brown lines. Members of the *Encyclia diota* complex tends to occupy dry, seasonally deciduous forests, from Mexico (northwestern Oaxaca) to northern Nicaragua, generally at medium to high altitudes (600–2000 m).

Historically, whether *Encyclia diota* represents one or more species has generated considerable disagreement. Some taxonomists propose the existence of at least two species (*E. diota* and *E. insidiosa* (Rchb. f.) Schltr.), a view we support; others suggest the complex consists of one species (consult Dressler 1976, for a historical review). These discrepancies are reasonable because, on the one hand, plants from different populations are, at first, difficult to distinguish from each other but, on the other hand, careful examination can show clear and consistent morphological differences between populations, strongly associated with a geographical component, a biological scenario that may require more than one species to be understood (Leopardi-Verde et al. in prep.).

We recently detected yet another species in this complex that shows differences in shape, size, and colors from others in the complex, which is here described and illustrated.

Materials and methods

Live plants were studied ex situ, from collections of German Carnevali and the Missouri Botanical Garden. We also examined 49 specimens housed at herbaria AMES, AMO, CICY, F, MEXU, MO, TEFH and W. Of these, 23 were of *Encyclia diota* and 21 of *E. insidiosa*. Acronyms of the herbaria follows Thiers (2013). The characters (vegetative and floral) used to describe the new species were determined from the fresh and dry specimens. In case of fresh materials and dry specimens, pictures of whole samples were

taken with a FUJIFILM FinePix S200EXR digital camera. Fresh flowers were dissected and digitized in a XL1600 EPSON scanner. For rehydration, herborized flowers were placed in a commercial detergent with ammonia for about 30–45 min, and then left in water for about one hour; afterwards they were dissected and mounted in a glass slide to digitize in a XL1600 EPSON scanner. Each specimen or its details were digitized with a scale. The cardboard file mounted records were scanned directly. All measures (height, length and width of pseudobulb, leaves, length of the inflorescence and its branches, etc.) were taken with the software ImageJ (Schneider 2012).

Data resources

The data underpinning the analysis reported in this paper are deposited at GBIF, the Global Biodiversity Information Facility, http://ipt.pensoft.net/resource.do?r=encyclia_diota_complex.

Taxonomy

***Encyclia inopinata* Leopardi, Carnevali & G.A.Romero, sp. nov.**

urn:lsid:ipni.org:names:77151882-1

Figures 1, 2

Type. MEXICO. **Oaxaca:** Distrito de Tlaxiaco, Municipio de Santiago de Yosondúa, 2.8 km. al SSE en línea recta (4–5 mm. por carretera) de Santiago de Yosondúa por la vía a Yerba Santa, 16°49'18.26"N, 97°35'11.63"W, 1267 m, 24/VI/2010, *G. Carnevali* & *C. Leopardi* 7139 (Holotype CICY; isotypes AMES, AMO).

Diagnosis. *Encyclia inopinata* is similar to *E. diota*, but it can be distinguished by its flowers with longer and narrower sepals ($1.8 \pm 0.1 \times 0.63 \pm 0.03$ cm in *E. inopinata* versus $1.48 \pm 0.14 \times 0.65 \pm 0.06$ cm in *E. diota*) and petals ($1.7 \pm 0.05 \times 0.59 \pm 0.05$ cm in *E. inopinata* vs. $1.36 \pm 0.19 \times 0.81 \pm 0.13$ cm in *E. diota*), and the labellum with narrow lateral lobes (0.18 ± 0.02 in *E. inopinata* vs. 0.41 ± 0.10 cm in *E. diota*). Other characters that differentiate these two species are the coriaceous sepals, pink callus, and white anther of *Encyclia inopinata* (versus fleshy-leathery sepals, white callus, and yellow anther of *E. diota*).

Description. Epiphytic herb, 30–42 cm tall, up to 80–90 cm including the inflorescence. Rhizome short and fibrous. *Pseudobulbs* 5.0–8.0 \times 3.9–4.5 cm, clustered, ovoid to pyriform, apically 2–3-leaved, green and smooth when young, covered with papery sheaths that eventually defibrate and disintegrate, when old sometimes stained with maroon or purple. *Leaves* 34–38 \times 2.8–3.5 cm, linear-oblong to oblong-ligulate, subacute, coriaceous, conduplicate at the base, dark green to purple tinged with central nerve marked mainly on abaxial face. *Inflorescence* 60–90 cm long, terminal, erect, racemose or paniculated, when panicles with 3–5 branches of 2.6–11 cm long, each

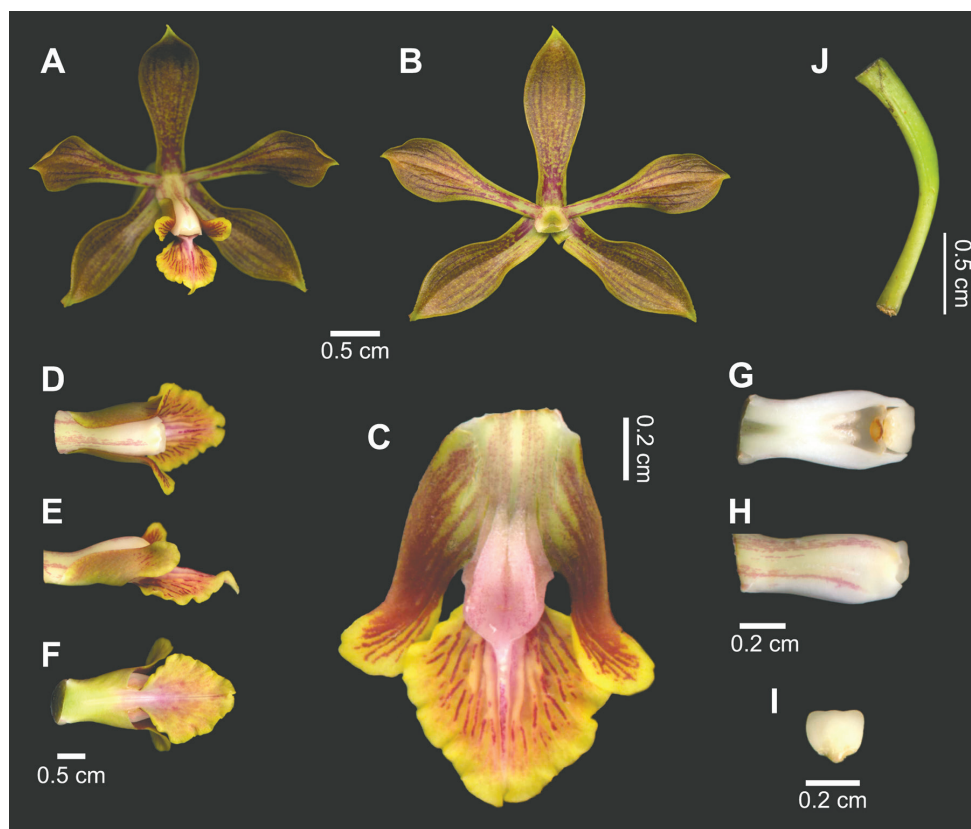


Figure 1. *Encyclia inopinata*. **A** Flower in frontal view **B** Perianth **C** Spread labellum **D–F** Column and labellum, in natural position, in dorsal (**D**) lateral (**E**) and ventral (**F**) views **G–H** Column in ventral (**G**) and lateral (**H**) views **I** Anther **J** Pedicellate ovary. Based on the holotype.

branch with 3–8 flowers, the entire inflorescence with up to 50 flowers; peduncle slender but strong, smooth, usually green, with adpressed sheaths of 0.9–1.4 cm long, that become smaller toward the apex; bracts inconspicuous, triangular of 0.2–0.5 cm long; pedicellate ovary 1.3–1.7 cm long, smooth. *Flowers* resupinate, showy, 3.0–3.4 cm diameter (between the tips of the petals); sepals and petals coriaceous, bronze-green, veins marked with dark purple lines; labellum green towards the base and pale, dull yellow-green toward the apex, with reddish-brown lines, the central lobe with well developed keels that reach the apex, of these the most conspicuous is the central one, lateral lobes with reddish brown lines that extend almost to the apex, lateral lobes free of the central lobe, pale pink callus; column creamy white with reddish-brown spots and lines; sepals similar, oblanceolate, acute, the laterals oblique, dorsal sepal 1.7–1.9 × 0.60–0.65 cm, lateral sepals 1.7–1.9 × 0.60–0.65 cm; petals 1.65–1.73 × 0.57–0.60 cm, obovate-spatulate to narrowly obovate-spatulate, with a conspicuous claw towards the base of 0.64–0.68 × 0.10–0.16 cm, acute to acuminate. *Labellum* 1.25–1.35 × 0.9–1.1 cm, 3-lobulate, free of the column except at the base, central lobe 0.5–0.7

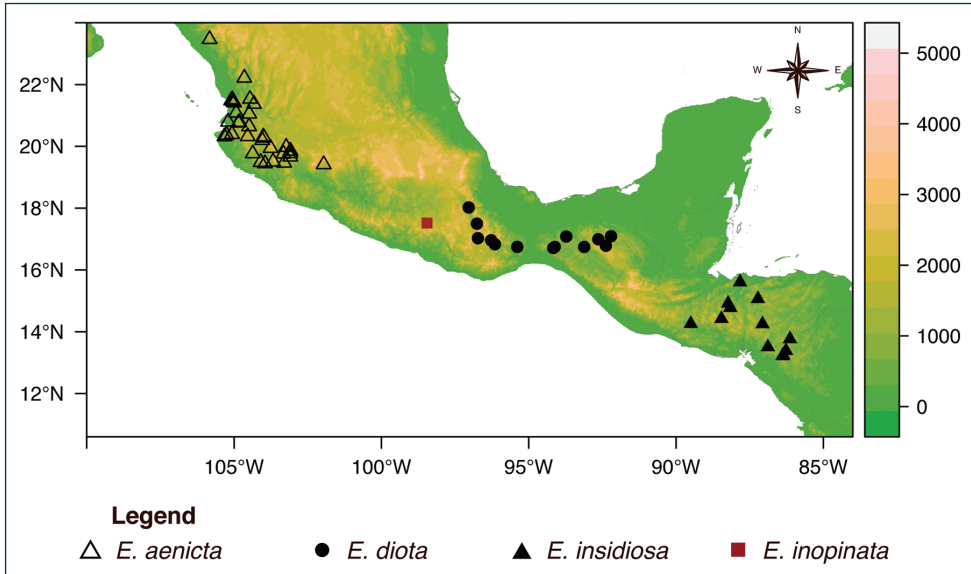


Figure 2. Distribution of species of the *Encyclia diota* complex. The color bar in the right side represents the altitude in meters.

× 0.6–0.8 cm, ovate, shortly acuminate; lateral lobes 0.80–0.90 cm long, 0.17–0.20 cm wide in the middle portion and 0.4–0.5 cm wide in the portion that lies between the base of the labellum and which separates within the central lobe, oblong, rounded towards the apex, separated of the central lobe by a sinus of ca. 0.1 cm width; in natural position lateral lobes are reflexed at the apex, and embrace the column; callus 0.45–0.49 × 0.24–0.28 cm, sub-rhombic, hirsute, consisting of two keels separated by a conspicuous sulcus, which widens slightly and forms a fovea, these keels converge towards the apex of the callus extending into the blade of the central lobe of the labelum as a keel that reaches the apex. *Column* 0.6–0.7 × 0.2–0.3 cm, semi-cylindrical, straight, ventral outline slightly clavate, wingless; anther 0.18–0.22 × 0.18–0.22 cm, white; pollinia 4, yellow, separated into groups of two, yellow caudicles; stigmatic surface 0.23–0.29 × 0.19–0.24 cm, subquadrate; rostellum 0.060–0.064 × 0.149–0.153 cm, semicircular. *Capsule* not seen (Figure 1 A–J).

Additional specimens examined. MEXICO. **Oaxaca:** El Llano, IV/1964, *Miller* sub *G. Pollard E-34* (AMO; card); km. 230 Puerto Escondido Highway to Oaxaca, V/1964, *G. Pollard E-45* (AMO; card); km. 154 Puerto Escondido Highway, 28/I/1969, *G. Pollard E-209-D* (AMO; card); Municipio San Juan Cacahuatepec, ca. 10.5 km north of San Juan Cacahuatepec, 15/III/1967, *G. Pollard E-209-C* (AMO; card).

Distribution and ecology. *Encyclia inopinata* has been reported only from Oaxaca state near the pacific slope from north of Puerto Escondido to north of San Juan Cacahuatepec (near the border with the Guerrero state) in deciduous forest, ca. 1200 m (Figure 2). It usually grows as a lithophyte. This species appears to be rare. It blooms between March and July.

Etymology. From the Latin *inopinatus*, unexpected, in reference to the surprise that we felt when first seeing the new species in bloom and realizing that it was an undescribed species in the *E. diota* complex.

Comments. Dressler and Pollard (1974: 130) suggested that a population of *Encyclia aenicta* in Oaxaca “tend[s] to have longer and wider lateral lobes and also tends to be more yellowish in color, suggesting, some hybridization with *E. diota*.” These authors implied that, size-wise, this entity was more similar to *E. aenicta* than to *E. diota*. The locality and characters showed by Dressler and Pollard (1974: 130) strongly suggests that they were referring to a population of what is here proposed as *E. inopinata*. Another source containing information about an entity similar to *E. inopinata* is the “Notes on *Encyclia*”, and unpublished manuscript of G. Pollard (housed at the AMO library). Tome 4 (“N to O”), page 69, describes a specimen that matches well our concept of *E. inopinata*. This manuscript also has additional cards (E-34 y E-45, p. 70 and 72 respectively) and pictures (p. 71) showing specimens that, again, match well the new species proposed herein.

Hybridization, most likely, has played an important role in the evolution and diversification of *Encyclia* (Dressler and Pollard 1974, Leopardi-Verde 2014). However, in this case, it is difficult to support the hypothesis of a cross between *E. diota* and *E. aenicta* as the origin of *E. inopinata* (Dressler and Pollard 1974: 130). We strongly reject this hypothesis considering that there is no contact zone between these taxa (Figure 2) and, in addition, the lack of morphological intermediacy between the hypothetical parents of such hybrid.

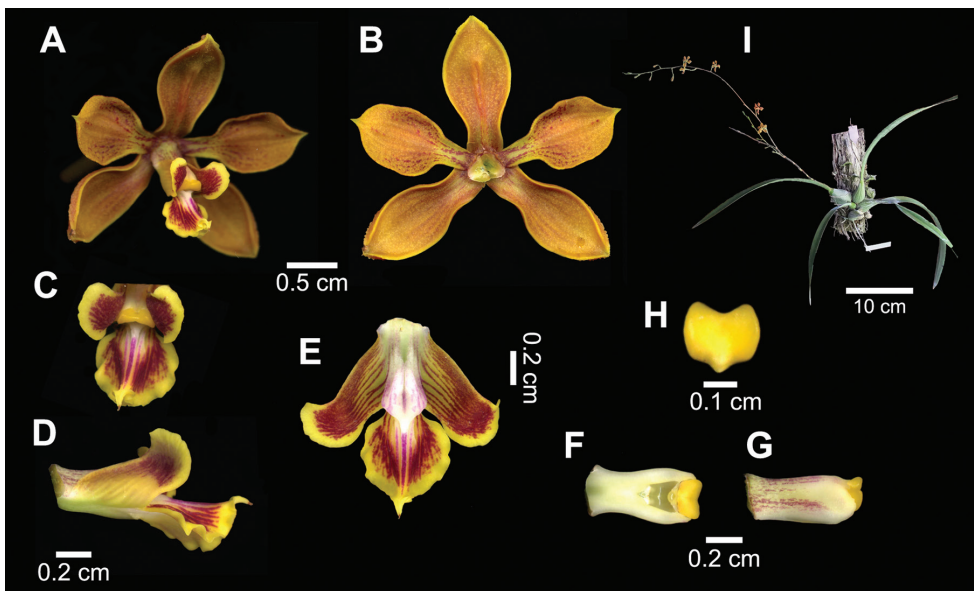


Figure 3. *Encyclia diota*. **A** Flower in frontal view **B** Perianth **D–F** Column and labellum, in natural position, in frontal (**C**) and lateral (**D**) views **E** Spread labellum **F–G** Column in ventral (**F**) and lateral (**G**) views. **H**, Anther. **I**, Plant. Based on Leopardi 337 (CICY).



Figure 4. *Encyclia insidiosa*. **A–B** Flower in frontal view of different phenotypes **A** from Nicaragua **B** from Honduras **C** Dissection of a flower **A** based on Stevens 20535 (MO), photo O. Montiel **B** based on House s.n., photo P. House **C** Drawn by C. Leopardi from a re-hydrated flower with the aid of a lucid camera, based on *Edwards 410* (AMES).

Finally, *Encyclia inopinata* resembles *E. diota* in floral colors, but the texture and proportions of the flowers are very different (see diagnosis above). *Encyclia inopinata* is also similar to *E. insidiosa*, an entity from Central America (ranges from Nicaragua to northern Guatemala). *Encyclia inopinata* and *E. insidiosa* can be discriminated by the tendency of the second to have sepals and petals dirty ochre to chocolate, whereas in *E. inopinata* these structures are bronze-green. The anther in *E. insidiosa* is yellow whereas in *E. inopinata* it is white or creamy white. The sepals and petals in *E. insidiosa* are shorter than in *E. inopinata* (1.54–1.68 cm versus 1.7–1.9 cm). The labellum of *E. insidiosa* and *E. inopinata* are similar in length, but in the former is wider (1.22–1.38 × 1.31–1.61 cm versus 1.25–1.35 × vs. 0.9–1.1 cm).

1 Sepals and petals fleshy-leathery, ochre, broadly spatulate, usually rounded or sub-squared towards the apex. Petals less than 1.5 cm long and more than 0.8 cm wide (ratio length/width in petals less than 1.9). Lateral lobes of the labellum ca. 0.9 ± 0.12 cm long and 0.4 ± 0.10 cm wide in the apical portion..... *E. diota* (Figure 3)

– Sepals and petals leathery or coriaceous, brown or bronze, obovate-spatulate to narrowly-obovate-spatulate, usually acute towards the apex. Petals more than 1.6 cm long and less than 0.7 cm wide (ratio length/width in petals more than 2.0). Lateral lobes of the labellum with ca. 0.8 ± 0.06 cm long or less and 0.3 ± 0.05 cm width in the apical portion..... **2**

2 Plants of Central America. Petals 1.6 cm long, rare 1.7 cm (ratio length/width: 2.5 or less), dirty ochre to chocolate. Labellum more than 1.3 cm wide (ratio length/width: less than 0.95). Callus white. Anther yellow *E. insidiosa* (Figure 4)

– Plants of Oaxaca (Mexico). Petals 1.8 cm long or more (ratio length/width: 2.8 or more), bronze-green. Labellum less than 1.1 cm wide (ratio length/width: more than 1.2). Callus pink. Anther white or creamy white..... *E. inopinata* (Figure 1)

We are grateful to Rodrigo Duno de Stefano for a careful review of a first draft of this manuscript. We would also like to thank Olga Martha Montiel (MO) for sending photographs of *Encyclia* specimens from Nicaragua, Paul House for sending pictures from specimens of Honduras, and the curators of AMO, F, MEXU, MO, and TEFH for allowing access to their collections. Also we are in debt to Angel Vale González (University of Vigo) for his careful reviews and comments. The AMO herbarium was particularly helpful with specimen data and in unraveling Glenn Pollard's localities of the new species and related taxa. CL acknowledges support received from Secretaría de Educación Pública of Mexico (Subsecretaría de Educación Superior) and the Universidad de Colima for the postdoctorate scholarship under the Programa para el Desarrollo Profesional Docente tipo superior (PRODEP). CONACyT partially funded this project through grant "Sistemática y Filogenia de *Encyclia* Hook. (Orchidaceae: Laeliinae), con énfasis en Megaméxico" (CB-2011-000000000168640), awarded to GC. The American Orchid Society provided funds for the project "Systematics and evolution of *Encyclia* Hook. s.s. (Orchidaceae: Laeliinae) with emphasis in Megamexico" (to G.C.).

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Homalium glandulosum (Salicaceae), a new species from Vu Quang National Park, North Central Vietnam

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Academic editor: Irina Belyaeva | Received 10 October 2015 | Accepted 2 December 2015 | Published 12 January 2016

Citation: Tagane S, Nguyen VH, Ngoc NV, Son HT, Toyama H, Yang C-J, Yahara T (2016) *Homalium glandulosum* (Salicaceae), a new species from Vu Quang National Park, North Central Vietnam. PhytoKeys 58: 97–104. doi: 10.3897/phytokeys.58.6816

Abstract

Homalium glandulosum Tagane & V. H. Nguyen, from Vu Quang National Park in northern Vietnam, is newly described. This species is characterized by distinct glands, often stalked, at the base of the lamina and along the margin of the stipules and bracteoles. Illustrations, DNA barcodes of the two regions of *rbcL* and *matK*, and a key to the species of *Homalium* in Vietnam are also provided.

Keywords

Homalium, new species, Salicaceae, taxonomy, Vietnam, Vu Quang National Park

Introduction

Homalium Jacq., with more than 150 species, is a genus of woody plants widely distributed in the tropics of the world, with the center of diversity in Southeast Asia and Madagascar (Sleumer 1954, 1973, Applequist 2013). The genus is characterized by bisexual flowers with free petals and sepals, obconical calyx tube adnate to ovary in the

lower part (i.e., semi-inferior ovary) and disk glands. It was previously classified in Flacourtiaceae (e.g. Sleumer 1954, Lescot 1970, Sleumer 1985, Yang and Zmarzty 2007) or Homaliaceae (Gagnepain 1921), but Chase et al. (2002) included it in Salicaceae *sensu lato* based on phylogenetic analyses of plastid *rbcl* DNA data.

In Vietnam, 11 species of *Homalium* have been known: *H. caryophyllaceum* (Zoll. & Moritz) Benth., *H. ceylanicum* (Gardner) Benth. (synonym, *H. balansae* Gagnep., *H. hainanense* Gagnep.), *H. cochinchinense* (Lour.) Druce (synonym, *H. digynum* Gagnep., *H. fagifolium* (Lindl.) Benth.), *H. dasyanthum* (Turcz.) W. Theob. (synonym, *H. griffithianum* Kurz), *H. dictyoneurum* (Hance) Warb., *H. grandiflorum* Benth., *H. mollissimum* Merr., *H. myriandrum* Merr., *H. petelotii* Merr., *H. phanerophlebium* F. C. How & W. C. Ko, and *H. tomentosum* (Vent.) Benth. (Gagnepain 1921, Lescot 1970, Hô 1999, Yang and Zmarzty 2007). Here, we describe an additional species, *H. glandulosum* Tagane & V. H. Nguyen, from Vu Quang National Park, Ha Tinh Province, North Central Vietnam.

Vu Quang National Park covers an area of ca. 56,000 ha containing an elevation gradient of over 2,000 m, from 30 m in the lowlands to 2,286 m at the summit of Mt. Rao Co (Rào CỎ), on the border with Laos (Vu Quang National Park Management Board 2014: see Fig. 1). The vegetation is diverse along the elevational gradient and Kuznetsov (2001) described five major forest types: lowland forests (alt. 10–300 m),



Figure 1. Location of Vu Quang National Park, Vietnam.

hill forest (alt. 300–1,000 m), medium montane forest (alt. 1,000–1,400 m), montane forest (alt. 1,400–1,900 m) and upper montane forest (alt. 1,900–2,100 m). From the national park, 1,678 species of vascular plants, 94 species of mammals, 315 species of birds, 58 species of reptiles and 31 species of amphibians, including many endemic and rare species, have been recorded, indicating that Vu Quang National Park is one of the centers of biodiversity in Vietnam (Eames et al. 2001, Tordoff et al. 2004, Vu Quang National Park Management Board 2014).

During our botanical inventory in Vu Quang National Park in July 2015, we discovered a previously undescribed species of the genus *Homalium*. Here we describe the species as *H. glandulosum*, accompanied with illustrations, DNA barcodes of the two plastid regions *rbcl* and *matK* (CBOL Plant Working Group 2009), and a key to the species of *Homalium* in Vietnam. DNA amplification and sequencing were performed according to published protocols (Kress et al. 2009, Dunning and Savolainen 2010, Toyama et al. 2015).

Taxonomy

Homalium glandulosum Tagane & V. H. Nguyen, sp. nov.

urn:lsid:ipni.org:names:77151885-1

Figures 2, 3

Diagnosis. Similar to *H. petelotii* Merr., but differing in having distinct glands, often stalked, at base of lamina and along margin of stipules and bracteoles, and spreading hairs on rachis of inflorescences, calyx tubes, sepals and petals (vs. glabrescent or only short appressed hairs in *H. petelotii*). Also, similar to *H. cochinchinense* (Lour.) Druce and *H. mollissimum* Merr. but distinguished from these two by the distinct glands mentioned above and very sparsely pubescent branches and petioles (vs. pubescent to densely pubescent).

Type. VIETNAM. Ha Tinh Province; Vu Quang National Park; along the trail to the summit; in hill forest, alt. 453 m, 18°16'25.3"N, 105°21'40.8"E, 25 July 2015, Tagane S., Yahara T., Toyama H., Nguyen N., Yang C. J. & Nguyen H. V3735 (holotype KYO!; isotypes BKF!, DLU!, FU!, NTU!, the herbarium of Vu Quang National Park!).

Description. Small tree, 9 m tall, DBH 15.6 cm; bark gray-brown; branchlets very sparsely pubescent, soon glabrous, with many lenticels, which are narrow to broadly elliptic, 0.3–0.9 × 0.1–0.25 mm, whitish; young twigs blackish when dry, old twigs grey-brown. Leaves: simple, alternate, petiole 2.5–5 mm long, sparsely pubescent when young, blackish when dry; leaf blade ovate to elliptic-ovate or oblong-ovate, (2.4–)3.5–9.8 × (1.0–)1.2–3.1 cm, papery, very sparsely pubescent on both surfaces, apex acuminate to acute, rarely obtuse, with a gland on tip, base cuneate, with 2–5 pairs of stalked glands at border with petiole, margin crenulate with glandular teeth; midribs prominent on both surfaces, glabrescent, secondary veins 6–7 pairs, arising at an angle of 40–45 degrees from the midrib, slightly prominent on both surfaces, tertiary veins reticulated, visible when dry. Stipules narrowly triangular, ca. 5 × 1 mm,

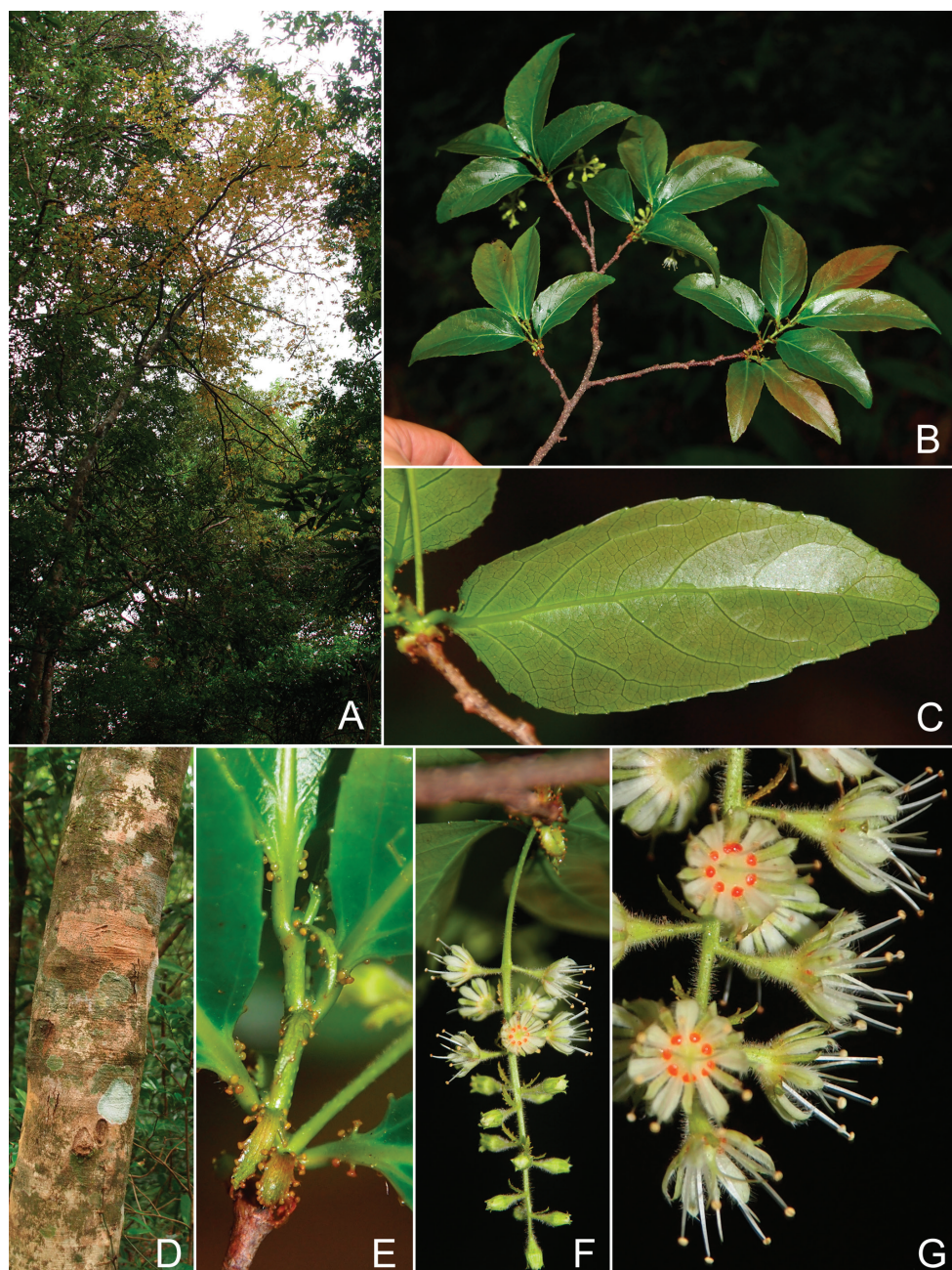


Figure 2. *Homalium glandulosum* Tagane & V. H. Nguyen: **A** habit **B** a flowering branch **C** abaxial leaf surface **D** bark **E** apical branch showing glandular stipules and leaf base **F** inflorescence **G** close up view of flowers.

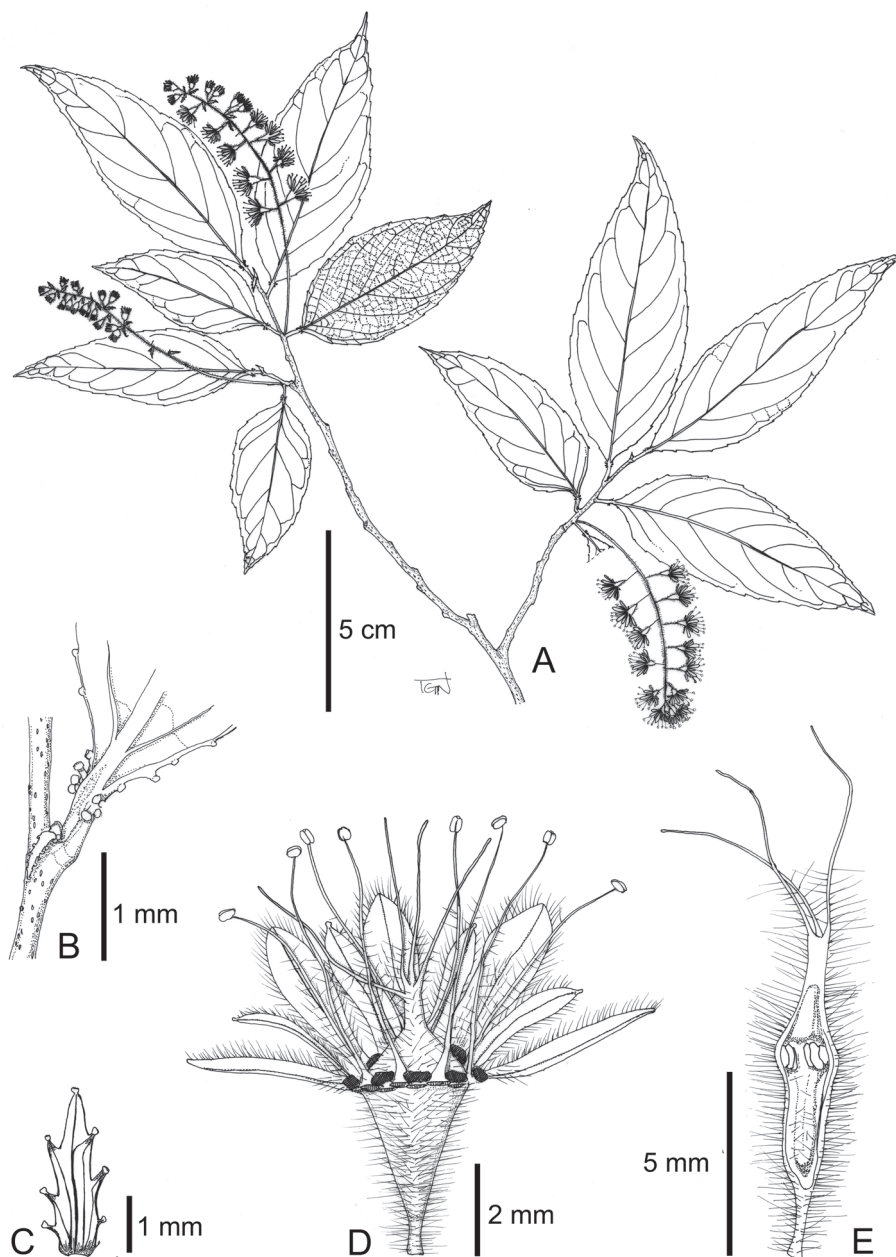


Figure 3. *Homalium glandulosum* Tagane & V. H. Nguyen: **A** flowering branch **B** stipule and base of a leaf **C** bracteole **D** flower **E** longitudinal section of gynoecium.

thinly papery, with 4–6 glandular teeth per side, glands often stalked, apex acute, with a gland on tip, blackish when dry, very sparsely pubescent, caducous. Inflorescences axillary, pendant, racemes or racemiform panicles with flowers borne singly on rachis or in clusters of up to 3 sometimes on short branches, 4–9 cm long, 7–20 flowered; rachis densely pubescent with spreading hairs except glabrous and lenticellate basally; bracts caducous, not seen. Pedicels 2.5–3.5 mm long, densely pubescent with spreading hairs; bracteoles narrowly ovate, 2.5–3 mm long, margin with 3–5 stalked glands per side, glabrous except near base, caducous. Flowers fragrant, 6–8 mm in diam.; calyx tube ca. 2.5 mm long, densely pubescent with spreading hairs; sepals 8, narrowly oblanceolate, ca. 3×0.5 mm long, membranous, with conspicuous midvein, light green *in vivo*, glabrescent except near basal part on both surfaces and ciliate margin, hairs spreading, 0.6 mm long, apex apiculate, with a gland on tip; petals 8, oblanceolate, 3.5×1.1 mm, membranous, with conspicuous midvein and lateral veins, whitish *in vivo*, glabrescent except lower 1/3 on both surfaces, margin ciliate with spreading hairs, hairs ca. 0.6 mm long, apex obtuse to acute. Disk glands 8, ca. 0.3 mm in diam., orange *in vivo*, black when dry, stipitate, stalk ca. 0.15 mm long, sparsely hairy. Stamens 8, filaments ca. 5.5 mm long, sparsely spreading hairy in lower 3/5; anthers ca. 0.4 mm long, longitudinally and extrorsely dehiscent. Ovary semi-inferior. Styles 3 or 4, filiform, ca. 5 mm long, united in lower 1/3, hairy in lower 1/2, hairs spreading; placentas 3 or 4, each with (3–)4 ovules, sparsely hairy inside. Fruits not seen.

Distribution. So far known only from the type locality.

Habitat and Ecology. Rare in hill evergreen forest, at alt. 453 m. Flowering specimens were collected in July.

GenBank accession no. Tagane et al. V3735: LC0901208 (*rbcL*), LC0901207 (*matK*). The BLAST similarity search based on the *matK* sequence of *H. glandulosum* resulted in homology as high as 834/835, 773/774, 767/768 bp with the sequence of *H. cochinchinense* (GenBank accession no. HQ415362, KP093841, KP093840, respectively) in the DNA database.

Etymology. The specific epithet '*glandulosum*' reflects the existence of distinct glands, often stalked, on stipule, leaf base and bracts.

Conservation status. Data Deficient. Only one flowering individual was found in a protected area of Vu Quang National Park. Further efforts for finding additional individuals/populations are needed to evaluate its conservation status.

Note. In Vu Quang National Park, another species of *Homalium*, *H. cochinchinense*, occurs in lowland forest (e.g., alt. 70 m, 27 July 2015, Tagane et al. V3818 (BKF!, DLU!, FU!, NTU!, the herbarium of Vu Quang National Park!). The species is easily distinguished as in the above diagnosis and the following key.

Key to the species of *Homalium* in Vietnam (modified from Lescot (1970), Sleumer (1985) and Yang and Zmarzty (2007))

1a	Stamens solitary before each petal	2
1b	Stamens 2 or more before each petal	8
2a	Styles dentiform, less than 1 mm long	<i>H. tomentosum</i>
2b	Styles filiform, 2–5 mm long	3
3a	Petals less than 2 mm long	<i>H. ceylanicum</i>
3b	Petals 3–4 mm long	4
4a	Stipules, leaf bases and bracts with stalked glands	<i>H. glandulosum</i>
4b	Stipules, leaf bases and bracts without stalked glands	5
5a	Petioles 8–15 mm long; leaves with acumen ca. 10 mm or more; leaf blade drying blackish brown	<i>H. phanerophlebium</i>
5b	Petioles less than 7 mm long; leaves with acumen 9 mm or less; leaf blade not drying blackish (i.e. reddish brown to dark greyish brown)	6
6a	Inflorescences glabrescent or pubescent only with short appressed hairs	<i>H. petelotii</i>
6b	Inflorescences pubescent with spreading trichomes	7
7a	Abaxial surface of leaf pubescent on midrib and lateral veins only	<i>H. cochinchinense</i>
7b	Abaxial surface of leaf sparsely to densely pubescent throughout ...	<i>H. mollissimum</i>
8a	Stamens partly inserted on the lower part of the petals; sepals manifestly accrescent after anthesis	9
8b	Stamens inserted strictly between the disk glands; sepals not or slightly accrescent after anthesis	10
9a	Bracts lanceolate-oblong, 4–8 mm long, caducous	<i>H. grandiflorum</i>
9b	Bracts ovate-flabelliform, 5–6 mm long, persistent	<i>H. dictyoneurum</i>
10a	Stamens consistently 2 before each petal	<i>H. dasyanthum</i>
10b	Stamens at least partly in fascicles of 3 or more	11
11a	Flowers with distinct pedicles of 3–5 mm long; calyx tube same length as the petals	<i>H. myriandrum</i>
11b	Flowers subsessile; calyx tube more than twice as long as petals	<i>H. caryophyllaceum</i>

Acknowledgements

The authors cordially thank the Vietnam Administration of Forestry and Vu Quang National Park for permitting our botanical inventory in the protected area. We thank the curators and staff of ANDA, BK, BKF, BM, BO, HN, K, L and P for kind permission to access herbarium specimens. We thank Keiko Mase for her help with DNA barcoding. We also thank two anonymous reviewers and the editors of the journal for their help and advice. This work was supported by the Environment Research and Technology Development Fund (S9) of the Ministry of the Environment, Japan.

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Two new species of *Siphocampylus* (Campanulaceae, Lobelioideae) from the Central Andes

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Academic editor: C. Morden | Received 27 October 2015 | Accepted 9 December 2015 | Published 12 January 2016

Citation: Lagomarsino LP, Santamaría-Aguilar D (2016) Two new species of *Siphocampylus* (Campanulaceae, Lobelioideae) from the Central Andes. *PhytoKeys* 58: 105–117. doi: 10.3897/phytokeys.58.6973

Abstract

Two species of *Siphocampylus* (Campanulaceae: Lobelioideae) from the Central Andes of Peru and Bolivia are described, illustrated, and discussed with reference to related species. One species, *Siphocampylus antonellii*, is endemic to high elevation grasslands of Calca, Peru, while the second, *S. siberiensis*, is endemic to cloud forests of Cochabamba, Bolivia. Both species are robust shrubs that produce tubular pink flowers that are likely pollinated by hummingbirds.

Keywords

Andean biodiversity hotspot, Asterales, Bolivia, centropogonid clade, Peru, South America, taxonomy

Introduction

While the subfamily Lobelioideae Burnett of Campanulaceae Juss. is cosmopolitan in its distribution, more than half of its ~1200 species are restricted to the Neotropics (Lammers 2007). Most of these species (~550/680) belong to the Andean-centered centropogonid clade, which comprises *Burmeistera* Triana (~120 species), *Centropogon* C. Presl (~210 species), and the mainland species of *Siphocampylus* Pohl (~220 species). This clade is unique within Lobelioideae for its combination of Neotropical distribution, woody habit, entire corolla tube (i.e., neither fenestrate nor dorsally cleft), and floral adaptation to pollination by either hummingbirds or nectar bats (Lagomarsino et

al. 2014; Lammers 2002; Muchhala and Lammers 2005). Within the centropogonid clade, *Siphocampylus* can further be distinguished by its capsular (vs. baccate) fruit. The genus, however, is not monophyletic (Antonelli 2008; Knox et al. 2008): in addition to the Caribbean species, which are distantly related to the centropogonid clade, its mainland species form at least 11 subclades that are polyphyletic with respect to the berry-producing *Centropogon* (Lagomarsino et al. 2014). This result is not surprising given the high degree of character overlap between *Centropogon* and *Siphocampylus*, which has frequently resulted in the incorrect filing of material in herbaria (Gleason 1921; Lammers 1998) and the occasional description of a new species to the incorrect genus or of uncertain placement (e.g., *C. dubius* [Zahlbr.] E. Wimm. for both scenarios) (Gleason 1921). The non-monophyly of these genera is largely due to the dynamic evolution of fruit-type within the clade: fleshy fruits have evolved approximately eight times from dry-fruited ancestors, likely as a result of migration to densely forested habitats (Givnish et al. 2005, 2009; Lagomarsino et al. 2014). While further phylogenetic information is necessary to begin to re-delimit generic boundaries to reflect evolutionary relationships within Neotropical Lobelioideae, *Siphocampylus* species are easily identified to genus within the confines of the current classification system, especially when fruiting material is available. Despite its non-monophyly, *Siphocampylus* remains a conspicuous, if poorly studied, component of the cloud forests and high elevation grasslands that comprise much of the tropical Andean global biodiversity hotspot (Myers et al. 2000). Future taxonomic and phylogenetic work focused on the centropogonid clade will undoubtedly result in the description of many new species and discovery of new clades defined by synapomorphies.

Here we describe two new species of hummingbird-pollinated *Siphocampylus*. Type specimens for both species were included in the most recent molecular phylogeny of the centropogonid clade, which is based on five plastid markers and includes relatively dense taxon sampling that spans all recognized taxonomic divisions, geographical occurrences, and morphological variation within Neotropical Lobelioideae (Lagomarsino et al. 2014). The phylogeny provides the information necessary to discuss these new species in relation to their closest evolutionary relatives. We additionally discuss similarities and differences of the species placed closely to their relatives in the most recent monograph of *Siphocampylus* (Wimmer 1943, 1953, 1968).

Methods

Field collections focused on Campanulaceae were conducted in Bolivia in November–December, 2011 and in Peru in November–December, 2012. Species identification and description of new species resulting from this fieldwork utilized many taxonomic references (Gleason 1921; Lammers 1998; León and Lammers 2006; Wimmer 1937, 1943, 1953, 1968) and collections at the following herbaria: A, BOLV, GB, GH, LPB, MO, MOL, NY, USM, and USZ. Herbarium acronyms here and throughout follow the *Index Herbariorum* (Thiers 2013 [continuously updated]).

Taxonomic treatment

Siphocampylus antonellii Lagom. & D. Santam., sp. nov.

urn:lsid:ipni.org:names:77151883-1

Figs 1–2

Diagnosis. *Siphocampylus antonellii* is similar to *S. elfriedii*, but differs in its smaller, linear-oblongate leaves, ventral corolla lobe >1.3 cm long, and pleasant, lemon-like odor emitted from living plants.

Type. PERU. Cusco: Calca, Lares, Calle entre Amaparaes y Suyu, Arriba de Amaparaes, 12°58'902"S, 077°50'W, 3799 m, 10 December 2012 (fl), L. Lagomarsino, D. Santamaria, J. Wells, F. Farro 400 (holotype: A!; isotypes: GB!, MO!, NY!).

Shrub 1.5 m tall, branching 20 cm above the base, with soft wood; branches 0.2–0.6 cm in diameter, solid and fistulose, light brown to reddish purple in living material, glabrescent or white-tomentose; internodes 0.2–1.0 cm long; latex white. Leaves spirally arranged, distributed evenly along the branches, producing lemon-like odor; petiole 0.1–0.5 cm long, sometimes sessile, villous, the trichomes whitish, adaxially canaliculate, abaxially rounded to triangular; lamina 3.8–5.2 × 0.3–0.55 cm, linear-oblongate, not rugose, appearing glabrous but densely pubescent with diminutive, whitish, stellate to echinoid trichomes; base attenuate to decurrent, sometimes with uneven sides; apex acuminate; margin sinuate, subentire, or diminutively dentate, 11–25 teeth per side, rounded to uncinatate, sometimes appearing as a glandular callosity; venation reticulate, with 5–10 pairs of lateral nerves, ascending, impressed or indistinct adaxially, flat abaxially. Flowers solitary, axillary, generally towards the apex of branch; pedicel 3.0–5.0 cm long, straight for almost the entire length, but curved below the hypanthium, cylindrical or flattened, densely pubescent, bibracteolate; calyx lobes 5, 0.7–1.6 × 0.1–0.12 cm, linear-oblongate, margins diminutively dentate with 3–5 teeth per side, densely pubescent on both surfaces, straight, the apex acuminate; corolla (2.8–) 3.9–5.1 cm long, tube pink with yellow to light green lines parallel to the lobes, lobes light green-yellow externally, light yellow to cream colored inside, completely pubescent externally, pubescent internally with stellate to echinoid trichomes; tube 2.7–3.5 × 0.4–0.6 cm, constricted at the base and widening distally, straight at anthesis; corolla lobes 5, lanceolate to narrowly triangular, apex acute to acuminate, the two dorsal lobes 1.0–1.6 cm long, the two lateral lobes 1.3–1.5 cm long, the ventral lobe 1.4–1.9 cm long; staminal tube 3.5–4.5 × 0.1 cm, straight, glabrous, cream-colored to light green in living material, exerted between the two dorsal lobes; anther tube 0.5–0.7 × 0.2–0.21 cm, dark gray, glabrous, ventral anthers 0.4–0.6 cm long, penicillate at the apex, the trichomes white or yellowish gold, dorsal anther 0.45–0.6 cm long, glabrous. Fruits not seen.

Distribution and habitat. *Siphocampylus antonellii* is endemic to Peru, where it grows on rocky slopes in puna habitat at ~3800 m in elevation. It is only known from the type collection.

Phenology. Individuals were collected in flower in December; the rest of the phenology of this species remains unknown.

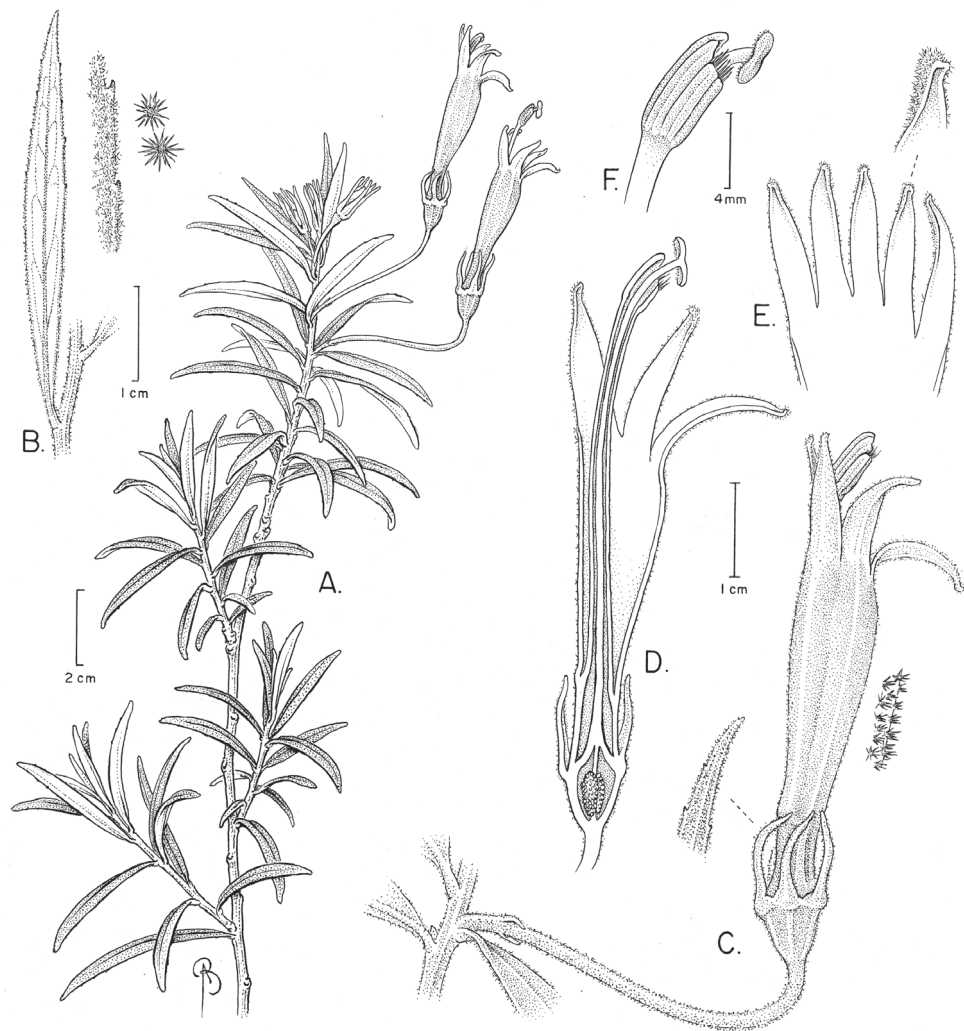


Figure 1. *Siphocampylus antonellii*. **A** Flowering branch **B** Leaf, abaxially, including detail of leaf margin and stellate hairs that cover surface **C** Staminate-phase flower, including bibracteolate pedicel, with detail of sepal and stellate hairs that cover the outer corolla surface **D** Longitudinal section of a pistillate-phase flower, showing the insertion of staminal tube to corolla, style and stigma as situated relative to the stamens, and bilocular ovary with axile placentation **E** Corolla lobe detail **F** Detail of anther tube, including apical hairs on ventral anthers, and stigma. Drawing by Bobbi Angel from the type.

Etymology. It is an honor to name this attractive species for Dr. Alexandre Antonelli (1978–), a biogeographer and phylogeneticist at the University of Gothenburg. Antonelli has made many important contributions to our understanding of Neotropical biodiversity through space and time, and to the evolution of various taxa, including Lobelioideae. His efforts in the latter brought the second author to the field in Costa

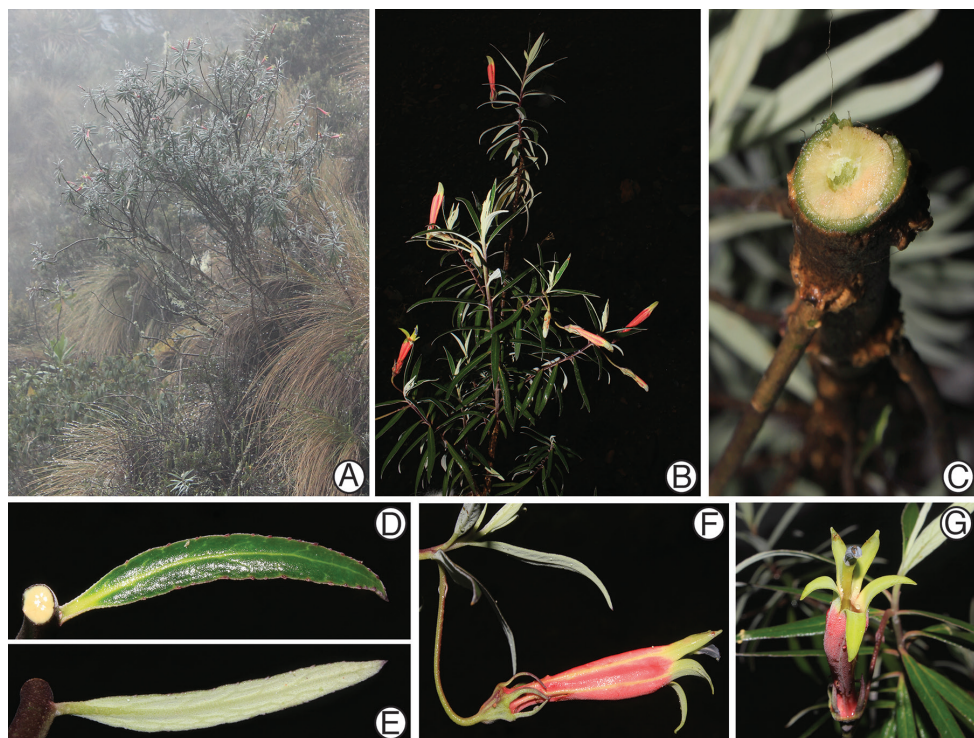


Figure 2. *Siphocampylus antonellii*. **A** Habit and high-elevation grassland (puna) habitat **B** Flowering branch **C** Cross-section of stem showing woody habit **D** Adaxial leaf surface **E** Abaxial leaf surface **F** Lateral view of flower in staminate phase **G** Anterior view of a flower, showing corolla aperture. All photos of the type collection, taken in the field by L. Lagomarsino.

Rica in 2005 in search of Campanulaceae, and helped to inspire the first author to study *Centropogon*, *Siphocampylus*, and *Burmeistera*.

Conservation status. *Siphocampylus antonellii* is endemic to a narrow stretch of high-elevation grassland (puna) in Calca, Peru, where it is locally abundant. Only a single population of this species is known, from which the type collection was made. Due to its small area of occurrence and the threat of future deforestation in its habitat, we tentatively consider this species to be Vulnerable (IUCN 2014). Its vulnerable status is further justified by its roadside occurrence, near major construction efforts.

Discussion. *Siphocampylus antonellii* is most similar to *S. elfriedii* E. Wimm. (Fig. 3C) and *S. parvifolius* E. Wimm., which are both also endemic to Peru. These species share a shrubby habit (Fig. 2A), generally high elevation occurrence ([1050–] 2100–3800 m), bibracteolate pedicels (Figs 1C, 2F), pink or pinkish-purple corolla tubes with yellow-green lobes (Figs 2F–G, 3C), glabrous anthers (except at the apex of the ventral anthers) (Figs 1F, 3C), and turbinate ovaries (Figs 1C, 2F, 3C). Both *Siphocampylus antonellii* and *S. elfriedii* produce echinoid trichomes, following Batterman and Lammers

Table 1. Differences between *Siphocampylus antonellii*, *S. elfriedii*, and *S. parvifolius*.

	<i>S. antonellii</i>	<i>S. elfriedii</i>	<i>S. parvifolius</i>
Leaf shape	Linear-ob lanceolate	Lanceolate	Lanceolate to oblanceolate
Leaf size	3.8–5.2 × 0.3–0.55 cm	5.0–7.4 × 1.1–1.9 cm	2.0 × 0.5 cm
Leaf margin	Margin sinuate, subentire, or diminutively dentate	Denticulate	Weakly crenulate
Sepal length	0.7–1.6 cm	0.7–1.4 cm	0.3 cm long
Sepal margin	Diminutively dentate	Denticulate	Entire or diminutively denticulate
Corolla length	(2.8–) 3.9–5.1 cm	3.9–4.6 cm	3.4 cm
Corolla indument	Pubescent	Pubescent	Glabrous
Dorsal corolla lobe length	1.0–1.6 cm	0.9–1.2 cm	1.1–1.4 cm
Ventral corolla lobe length	1.4–1.9 cm	0.5–1 cm	0.9–1.2 cm
Reference sheets	<i>L. Lagomarsino</i> 400 (A)	<i>L. Lagomarsino</i> 387 (GH); <i>J. L. Luteyn</i> & <i>M. L. Lebrón-Luteyn</i> 6395 (MO); <i>F. W. Pennell</i> 13841 (GH); <i>T. Plowman</i> & <i>E. W. Davis</i> 5126 (GH); <i>J. West</i> 7045 (GH)	<i>R. D. Metcalf</i> 30469 (A)

2004. However, *S. antonellii* can be easily distinguished by the differences enumerated in Table 1 and by the agreeable lemon-like smell that it emits.

This new species would be placed near *S. nobilis* E. Wimm. and *S. rosmarinifolius* G. Don in the dichotomous key of genus in Wimmer (1953). In addition to being restricted to Peru, these species share linear leaves, turbinate ovaries, and narrow corolla lobes. However, these two species have glabrous sepals and corolla (vs. pubescent in *S. antonellii*), ebracteolate, glabrous pedicels (vs. bibracteolate and pubescent), and different corolla colors: reddish orange with yellow lobes in *S. rosmarinifolius* and purple in *S. nobilis* (vs. pink with yellow-green lobes [Fig. 2F]). *Siphocampylus nobilis* can be further distinguished from *S. antonellii* by its vining habit (vs. shrubby), long, narrow leaves (6.0–8.0 × 0.2–0.3 vs. 3.8–5.2 × 0.3–0.55 cm), and glabrous branches, leaves, pedicels, and hypanthium (vs. pubescent [Fig. 1]). *Siphocampylus rosmarinifolius* can be further distinguished by its longer leaves (8.0–11.5 cm vs. 3.8–5.2 cm), the rugose, glabrous adaxial leaf surface (vs. not rugose and pubescent), and revolute leaf margins (vs. not revolute).

Molecular phylogenetic analysis places *S. antonellii* in a well-supported clade that includes *S. actinotrix* E. Wimm. (Fig. 3B), *S. elfriedii* (Fig. 3C), *S. vatkeanus* Zahlbr., *S. veteranus* E. Wimm. (Fig. 3A, D), and *S. rictus* Lammers; within this clade, *S. antonellii* is sister to *S. veteranus* (Lagomarsino et al. 2014). This clade as a whole is composed of generally tall, woody shrubs. The placement of *S. elfriedii* in this clade is not surprising, as it is quite similar to *S. antonellii* (see above). However, it is more difficult to find similarities with the remaining species, which can be easily distinguished from *S. antonellii* by a series of putative adaptations to pollination by bats: long pedicels



Figure 3. Closest relatives of *Siphocampylus antonellii*, based on molecular phylogeny of Lagomarsino et al. (2014). **A** Flower of *Siphocampylus veteranus* **B** Flower of *Siphocampylus actinothrix* **C** Flower of *Siphocampylus elfriedii* **D** Cross-section of main stem of *S. veteranus*, showing a much more robust habit than *Siphocampylus antonellii*, but similar wood structure. All photos taken in the field by L. Lagomarsino. **A, D** L. Lagomarsino et al. 388 **B** L. Lagomarsino et al. 403 **C** L. Lagomarsino et al. 387.

(7.0–15 cm), wide corolla apertures, and longer corollas (3.2–5.0 cm) that are generally dull in color (either green, cream-colored, white or yellowish, sometimes mottled with reddish pigmentation) (Fig. 3A–B). Additionally, these species have longer leaves (6.0–13.5 cm vs. 3.8–5.2 cm) and a glabrous or only sparsely pubescent corolla (but with echinoid-stellate pubescence in *S. actinothrix* [Fig. 3B]). Despite the similarities discussed above, *S. rosmarinifolius* falls outside of the clade that includes *S. antonellii* (Lagomarsino et al. 2014); *S. nobilis* and *S. parvifolius* have not yet been sampled in a molecular phylogenetic analysis.

***Siphocampylus siberiensis* Lagom. & D. Santam., sp. nov.**

urn:lsid:ipni.org:names:77151884-1

Figs 4–5

Diagnosis. *Siphocampylus siberiensis* is similar to *S. boliviensis*, but with a corolla tube lacking a constriction at its base and a hemispherical hypanthium.

Type. BOLIVIA. Cochabamba: Carrasco, en la entrada para Sunchal, cerca al rótulo “Unidad Educativa Manuela Gandarillas”, 17°47'267"S, 064°47'669"W,

2668 m, 18 December 2011 (fl & fr), *L. Lagomarsino, D. Santamaría & J. M. Mendoza 241* (holotype: A!; isotype: LPB, USZ).

Multi-stemmed shrub 3–4 m tall, branched, all branches arising from a single point at ground level, with soft wood, the bark suberose; branches 0.4–0.6 cm in diameter, fistulose, the youngest parts purple, brown when mature (greyish to whitish in dry material), glabrescent to tomentose; internodes 0.9–1.7 cm long; latex white. Leaves spirally arranged and generally clustered at the apex of branches, leaving prominent leaf scar after falling; petiole 0.3–0.7 cm long, glabrescent to tomentose with whitish trichomes, winged, adaxially canaliculate, abaxially more or less triangular with two ribs; leaf blade 10.5–19.5 × 2.9–4.6 cm, oblanceolate, adaxially tomentose and abaxially densely pubescent, the pubescence principally on the veins, trichomes simple, the base decurrent; apex acuminate; margin doubly dentate and ciliate, 75–95+ teeth per side, the teeth triangular; venation reticulate with 16–21 pairs of lateral nerves, lightly ascendant, impressed adaxially and elevated abaxially. Flowers solitary, axillary, generally towards branch apex; pedicel 4.5–9.4 cm long, straight, cylindrical, densely pubescent; bracteoles absent; hypanthium 0.5–0.8 × 0.3–0.4 cm, hemispherical, tomentose; calyx lobes 5, (0.8–) 1.0–1.4 × (0.2–) 0.3 cm, narrowly triangular, the margins ciliate, entire, pubescent on both surfaces, erect or recurved, the apex acuminate; corolla 3.5–3.8 cm long, completely pink, diminutively pubescent on both surfaces; corolla tube 0.9–2.2 × 0.7–0.8 cm, cylindrical for its entire length, a little wider apically than basally, straight at anthesis; corolla lobes 5, narrowly triangular, slightly falcate, the margins ciliate, the apex acute to acuminate, the two dorsal lobes 1.5 cm long, the two lateral lobes 1.4 cm long, the ventral lobe 1.4 cm long, staminal tube 3.0–3.8 × 0.1–0.2 cm, straight, sparsely pubescent, pink, exserted between the two dorsal lobes; anther tube 0.8–0.9 × 0.2–0.3 cm, gray in living material, glabrous except in the sutures between anthers, which are densely pubescent, the trichomes white, ventral anthers 0.6–0.8 cm long, penicillate at the apex, the trichomes white, the dorsal anthers 0.7–1.0 cm long, penicillate at the apex, the trichomes white. Fruit capsule, 5.0 × 1.0–1.2 cm, ca. 15-lobed, with external ridges, the calyx persistent; seeds not seen.

Distribution and habitat. *Siphocampylus siberiensis* is endemic to Bolivia, where it has been collected at the edge of the road at ca. 2700–2900 m in elevation in cloud forest.

Phenology. Individuals were collected in flower and fruit in December and in flower only in April; the rest of the phenology of this species remains unknown.

Etymology. The specific epithet of this species refers to the type locality, the Serranía de Siberia, a mountain range at the limit between the Cochabamba and Santa Cruz departments in Bolivia.

Conservation status. *Siphocampylus siberiensis* is known only from a single population in Serranía de Siberia in central Bolivia; this population is represented by the two cited collections. This species appears to be locally rare, and only one individual was encountered during our fieldwork. Due to its small area of occurrence and the threat of future deforestation in its habitat, we tentatively consider this species to be Vulnerable (IUCN 2014). Its vulnerable status is further justified by its roadside occurrence in montane cloud forest, a habitat type known to be particularly sensitive to human encroachment.

Discussion. *Siphocampylus siberiensis* can be recognized by its shrubby habit with multiple stems arising from a single point; leaves aggregated at the apex of branches (Fig. 4A); conspicuous venation (especially on the abaxial leaf surface) (Figs 4A, 5C); solitary flowers borne in the axil of leaves (Fig. 4A); light pink corolla with a tube that is cylindrical for its entire length (i.e., not basally constricted) (Figs 4B, D, 5F); anther tube that is densely pubescent in the sutures between individual anthers (Figs 4E, 5F); and fruits that are both ribbed and lobed (Figs 4F, 5E).

Molecular phylogenetic analysis places *S. siberiensis* in a clade that includes *S. tunarensis* Zahlbr., *S. tunicatus* Zahlbr., and *S. umbellatus* (Kunth) G. Don; this clade is closely related to *S. boliviensis* Zahlbr. and *S. sparsipilus* E. Wimm. (Lagomarsino et al. 2014) (Figs 5, 6). These species are all restricted to the Central Andes of Peru and Bolivia, with the exception of *S. umbellatus*, whose range also extends to Brazil. This clade is composed of robust shrubs or trees that are exceptionally tall for the centropogonid clade (Figs 5A, 6E–F), or rarely scandent subshrubs (*S. sparsipilus* and some collections of *S. boliviensis*), with ebracteolate pedicels, a shallow, hemispherical hypanthium (turbinate in *S. tunarensis*), and leaves that leave prominent scars after abscission (Fig. 4A) and have dentate margins and reticulate venation that is conspicuous on both surfaces, but especially the abaxial surface (Figs 4A, 5C). Both bright pink (*S. siberiensis*, *S. boliviensis*, *S. sparsipilus*) and dull colored (*S. tunarensis*, *S. tunicatus*, *S. umbellatus*) corollas are represented in this clade. This color variation, which is associated with different gross corolla morphologies, likely reflects adaptation to different pollinators (hummingbirds and bats, respectively) (Figs 5F–G, 6A–D).

Even though they are not the most closely related species, the pink, narrow flowers of *S. siberiensis* most closely resemble those of *S. boliviensis* and *S. sparsipilus*. However, the latter two species can be easily distinguished by their corollas that are constricted at the base (vs. not constricted) and much rounder hypanthium (vs. flattened at top). The other species in the immediate clade that includes *S. siberiensis* differ in their dull reddish (*S. tunarensis* [Fig. 6B]) or whitish-green (*S. tunicatus* [Fig. 6C], *S. umbellatus* [Fig. 6D]) corollas (vs. bright pink in *S. siberiensis*). *Siphocampylus tunicatus* and *S. siberiensis* are sister species that are vegetatively very similar, though their flowers are markedly different (Figs 4, 5, 6C, F). In addition to its green corolla, the former can be distinguished by its longer sepals (2.0–2.8 cm [Fig. 6C] vs. [0.8–] 1.0–1.4 cm [Figs 4B, D, 5F]) that are leaf-like (vs. not leaf-like) and its wider hypanthium (1.5–2.0 vs. 0.3–0.4 cm) (Fig. 6C). *Siphocampylus tunarensis* can be separated by its linear, revolute corolla lobes (Fig. 6B) (vs. narrowly triangular and not revolute [Figs 4B, 5F–G]) and short sepals (0.2–0.4 cm [Fig. 6B] vs. 1.0–1.4 cm [Fig. 5F]). Furthermore, while *S. siberiensis* is a robust shrub 3–4 m tall, *S. tunarensis* can grow to be a very tall tree (>10 m) with a diameter of more than 30 cm and is possibly one of the largest species of Campanulaceae in the Americas (Fig. 6E).

The species that is most superficially similar to *S. siberiensis*, *S. boliviensis*, is placed in the same couplet as *S. macrostemon* A. DC. in the dichotomous key to the members of the genus in Wimmer (1953). This markedly different species, which has not yet been sampled in molecular phylogenetic analysis, can be distinguished by its subsessile



Figure 4. *Siphocampylus siberiensis*. **A** Flowering branch, showing the persistent leaf scars and developmental procession of distal flower at anthesis to basal capsular fruit **B** Flower in pistillate phase, including detail of sepal with pubescence **C** Corolla lobe detail, including marginal pubescence **D** Longitudinal section of a pistillate phase flower, showing the insertion of staminal tube to corolla, style and stigma as situated relative to the stamens, and bilocular ovary with axile placentation **E** Anther tube in staminate-phase flower **F** Capsule with lobes and ridges. Drawing by Bobbi Angel from the type.

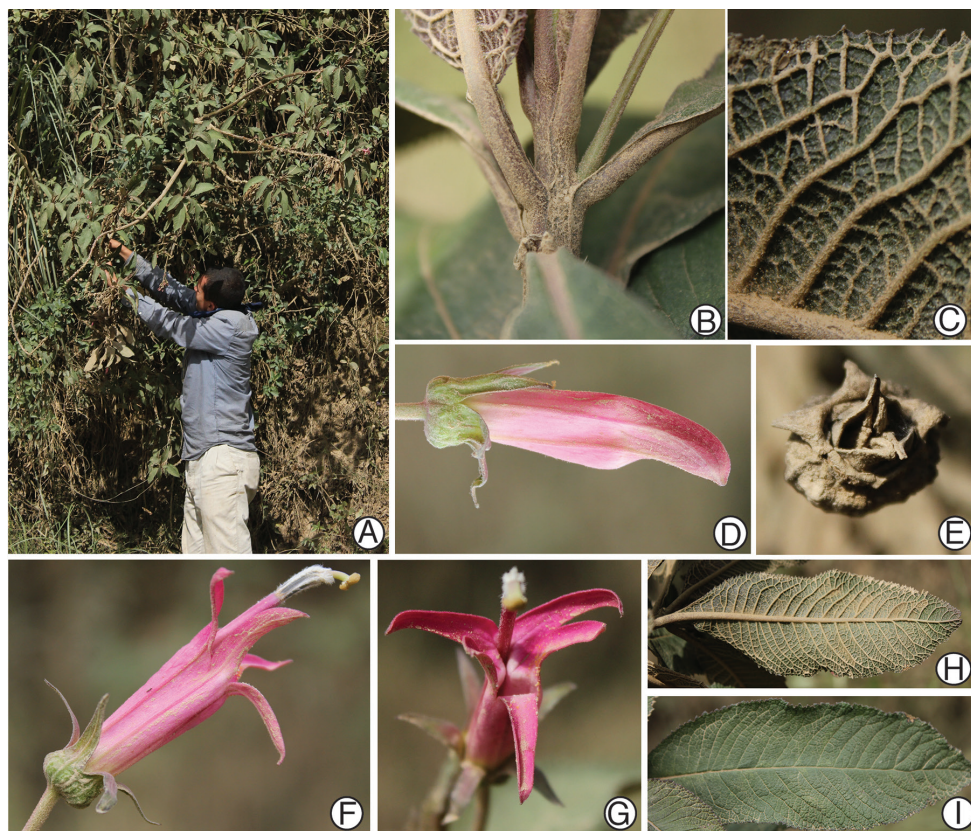


Figure 5. *Siphocampylus siberiensis*. **A** Habit **B** Detail of young stem **C** Detail of leaf margin and venation on abaxial leaf surface **D** Flower bud **E** Capsule **F** Lateral view of flower in pistillate phase **G** Anterior view of corolla, showing corolla aperture **H** Abaxial leaf surface **I** Adaxial leaf surface. All photos of the type collection, taken in the field by L. Lagomarsino; D. Santamaría-Aguilar is shown collecting the type in **A**.

leaves (vs. pedicels 0.3–0.7 cm long) that are smaller ($5\text{--}8 \times 1.31.5$ cm vs. $10.5\text{--}19.5 \times 2.9\text{--}4.6$ cm) and sparsely pubescent on the adaxial surface (vs. tomentose), minutely dentate leaf margins (vs. doubly dentate and ciliate), shorter pedicels (2.6–4.2 cm vs. 4.5–9.4 cm) that are bracteolate (vs. ebracteolate), and glabrous corolla (vs. pubescent). The other species most closely related to *S. siberiensis* fall into many disparate taxonomic units within the current classification scheme of the genus. This makes it difficult to place this new species in the context of Wimmer's taxonomy; this is likely due to this treatment's reliance on single, often arbitrary characters to designate groups.

The measurements of the calyx and corolla in parentheses correspond to *E. Fernández et al.* 3583 (MO). This specimen apparently has a white corolla, but otherwise corresponds to the species concept for *S. siberiensis* presented here.

Additional specimens examined. BOLIVIA: Cochabamba, Carrasco, Siberia, $17^{\circ}48'11''\text{S}$, $064^{\circ}46'12''\text{W}$, 2900 m, 16 April 2005 (fl), *E. Fernández et al.* 3583 (MO).

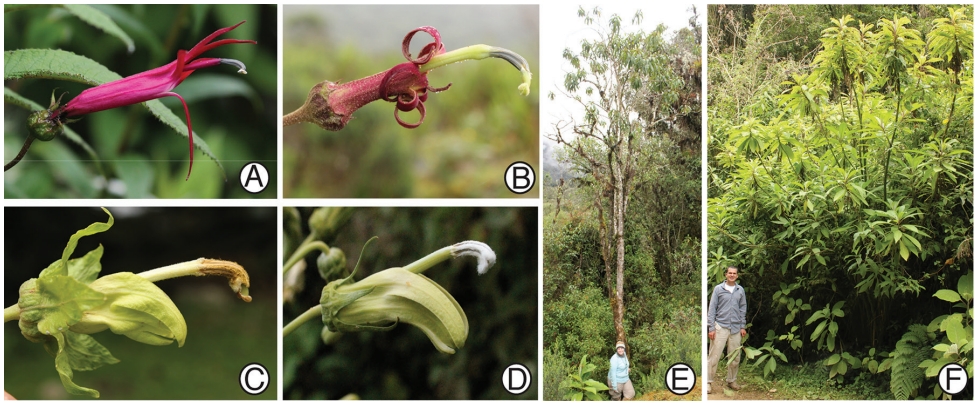


Figure 6. Closest relatives of *Siphocampylus siberiensis*, based on molecular phylogeny of Lagomarsino et al. (2014). **A** Flower of *Siphocampylus boliviensis* **B** Flower of *Siphocampylus tunarensis* **C** Flower of *Siphocampylus tunicatus* **D** Flower of *Siphocampylus umbellatus* **E** Habit of *Siphocampylus tunarensis*, shown with L. Lagomarsino **F** Habit of *Siphocampylus tunicatus*, shown with D. Santamaría-Aguilar. All photos taken in the field by L. Lagomarsino (**A–D, F**) and D. Santamaría-Aguilar (**E**). **A** *L. Lagomarsino et al.* 239 **B, E** *L. Lagomarsino et al.* 232 **C, F** *L. Lagomarsino et al.* 235 **D** *L. Lagomarsino et al.* 193.

Acknowledgements

We would like to thank the directors and curatorial staff at the following herbaria for permitting the use their collections: A, BOLV, GB, GH, LPB, MO, MOL, NY, SMF, and USZ. Funding was provided by an NSF Doctoral Dissertation Improvement Grant (DEB-1210401), Arnold Arboretum's Deland Award for Student Research, and the David Rockefeller Center for Latin American Studies to LPL. We thank Kanchi Gandhi for nomenclatural advice, Charles Davis, Clifford Morden, and an anonymous reviewer for comments that improved previous drafts of this manuscript, and Bobbi Angell for the beautiful line drawings of the two new species.

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Typification of Zapałowicz's names in *Aconitum* section *Aconitum*

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Academic editor: P. Stoev | Received 6 November 2015 | Accepted 10 December 2015 | Published 12 January 2016

Citation: Wacławska-Ćwiertnia K, Mitka J (2016) Typification of Zapałowicz's names in *Aconitum* section *Aconitum*. *PhytoKeys* 58: 119–126. doi: 10.3897/phytokeys.58.7110

Abstract

Hugo Zapałowicz described and named 27 taxa in *Aconitum* sect. *Aconitum*. Their names are typified here. Two of them (*A. berdaui*, *A. bucovinense*) are deemed correct for currently accepted species of the Carpathians, 24 are reduced to synonymy under five taxa, and for one no original material has been located. The correct place and exact date of their publication, which differs from those usually assumed, have been ascertained by bibliographic verification and the study of archival documents.

Keywords

Aconitum berdaui, *Aconitum bucovinense*, Carpathians, nomenclature, taxonomy, typification

Introduction

The species concepts and classification in *Aconitum* L. sect. *Aconitum*, as represented in the Carpathians, were proposed and discussed by Mitka (2000, 2002, 2003), Starmühler and Mitka (2001) and Novikoff and Mitka (2011). Cytogenetic information has been added by Ilnicki and Mitka (2009). Here, we consider the type specimens of relevant names published by Hugo Zapałowicz (1852–1917), applying the rules of the Melbourne Code (McNeill et al. 2011) and based on herbarium material deposited in KRAM.

To date it has been a generally accepted practice to cite all nomenclatural novelties that appear in Zapałowicz's "Conspectus florae Galiciae" from that Conspectus. However, we will show that, as correctly stated by Stafleu and Cowan (1988: 521) then confirmed by Köhler (2002), they should instead be cited from corresponding articles in "Rozprawy Wydziału Matematyczno-Przyrodniczego Akademii Umiejętności. Seria III. Dział B. Nauki biologiczne" (hereafter "Rozprawy"), which were published several months earlier than the "Conspectus". We verified that information by checking the available evidence (including printers' bills) related to the publication of the "Conspectus" and "Rozprawy" issues. We found that the date of publication of the relevant portion of the "Conspectus" is 22 December 1908, whereas for the "Rozprawy" issue it is 5 May 1908. Effective publication of the *Aconitum* names in question took place on the earlier date.

Materials and methods

Effective and valid publication of the *Aconitum* names that appear in the first fascicle of the "Rozprawy" (Zapałowicz 1908a) and in the second volume of the "Conspectus" (Zapałowicz 1908b) were assessed by study of the protologues. The corresponding herbarium material deposited in KRAM (Thiers 2011, <http://sweetgum.nybg.org/science/>), where a full set of Zapałowicz's plant collections is deposited, has been studied. In typifying these names we followed the rules of the International Code of Nomenclature for algae, fungi and plants (McNeill et al. 2012) and the recommendation made by McNeill (2014). In cases where a single specimen is known that was used by Zapałowicz, that particular specimen is nevertheless considered a lectotype, with the additional qualification: "or perhaps holotype".

Accepted names of the taxon, determined in conformity with Mitka (2003), appear in ***bold italics***. If different from the name here typified, they are added at the end of the entry [in square brackets, when they are heterotypic].

Results

In his treatment of *Aconitum* sect. *Aconitum* for the "Conspectus", Zapałowicz described and named 27 taxa: two hybrids, 9 varieties and 16 formae. Their names, with one exception, are typified here. Two hybrids (*A. berdaui*, *A. bucovinense*) are deemed correct for currently accepted species of the Carpathians, 24 are reduced to synonymy under five taxa, and for one no original material has been located.

Aconitum berdaui Zapał. in Rozpr. Wydz. Mat.-Przyr. Akad. Umiej., Dział B. Nauki Biol. 48: 88. 1908, *pro hybr.* (<http://ipni.org/urn:lsid:ipni.org:names:707195-1:1.2.2.1.1.1>). Protologue text: "In regione subalpina Tatrorum: in valle Kościeliska et altero loco non indicato (*Berdaui*), Podspady ad Jaworzynka

(*Rogalski*)". Lectotype (designated here): "Dol. Kościeliska, ?08.1855, leg. *Berdau*, det. *Zapałowicz* (16.02.1908), KRAM! (133482). Other syntypes: (1) "Podspady nad Jaworzynką, 25.07. (1878?), *A. Rogalski*" – KRAM! (133481); (2) "sine die, leg. *Berdau*, det. *Zapałowicz* (16.01.1908)" – KRAM! (133483).

Aconitum bucovinense Zapał. in Rozpr. Wydz. Mat.-Przyr. Akad. Umiej., Dział B. Nauki Biol. 48: 89-90. 1908, *pro hybr.* (<http://ipni.org/urn:lsid:ipni.org:names:707221-1:1.3>). Protologue text: „In montanis et subalpinis Bucovinae australis: Jakobeney, Pojana negri prope Dorna Kandreny (*Rehman*)". Lectotype (designated here, or perhaps holotype): "Dr *A. Rehman*: Exsiccata Florae Galiciensis; *Aconitum*; Jakobeni na Bukowinie [no date]; Nr LXXVI/3532" – KRAM! (132396).

Aconitum napellus f. *abnorme* Zapał. in Rozpr. Wydz. Mat.-Przyr. Akad. Umiej., Dział B. Nauki Biol. 48: 84. 1908. Protologue text: „Miętusia w Tatrach (*Kulczyński*)". Lectotype (designated here, or perhaps holotype): „Miętusia, 26.07.1875 r., leg. *W. Kulczyński*" – KRAM! (132273), first synonymized by Mitka (2003). – [*Aconitum firmum* Rchb. subsp. *firmum*].

Aconitum napellus f. *amoenum* Zapał. in Rozpr. Wydz. Mat.-Przyr. Akad. Umiej., Dział B. Nauki Biol. 48: 87. 1908. Protologue text: „Alpy Rodneńskie: Piatra rei u stóp skał wapiennych 1300-1350 m (*Zapałowicz*)". Lectotype (designated here, or perhaps holotype): „Piatra rei. Alpy Rodneńskie, 15.08.1907, leg. et det. *H. Zapałowicz*" – KRAM! (132300). – [*Aconitum czarnohorense* (Zapał.) Mitka].

Aconitum napellus var. *babiogorense* Zapał. in Rozpr. Wydz. Mat.-Przyr. Akad. Umiej., Dział B. Nauki Biol. 48: 85. 1908. Protologue text: „W krainie kosodrzewu Babiej Góry w Kościółkach 1565 m i t. d., wyjątkowo nad potokami nieraz bardzo nisko, np. nad Markowym Potokiem 725 m (*Zapałowicz*); a także na szczycie 1725 m (*Bobek*); Kuźnice w Zakopanem (*Jabłoński*). Okaz z Czarnej Hory (*Rehman*) bez bliższego oznaczenia miejscowości, planta cum filamentis glaberrima, bez żadnej wątpliwości tu należy. Ze względu na daleki wschód jest okaz ten bardzo ważny i pouczający; zacieśnia on związek między zachodnio – karpacką odmianą *babiogorense* m. a wschodnio-karpacką odm. *swidovense* sekcji II tak samo, jak niektóre formy pośrednie wymienione pod var. *czarnohorense* łączą tę ostatnią odmianę z zachodnio-karpacką odmianą *tatrense* m. sekcji III". Lectotype (designated here): „Babia Góra nad Markowym Potokiem, leg. et det. *H. Zapałowicz* (2.08.1877)" – KRAM! (132263). Other syntypes: (1) „Dyablak, ?08.1876, leg. *K. Bobek*" – KRAM! (132259); (2) „Zakopane, Kuźnice, 17.07. ?, leg. *W. Jabłoński*", KRAM! (132290); (3) „Czarna Hora, sine die" – KRAM! (132267). – [*Aconitum firmum* Rchb. subsp. *firmum*].

Aconitum napellus var. *bidgostianum* Zapał. in Rozpr. Wydz. Mat.-Przyr. Akad. Umiej., Dział B. Nauki Biol. 48: 83. 1908. Protologue text: „Koło Bydgoszczy". Lectotype (designated here, or perhaps holotype): „Okolice Bydgoszczy, Czerszkówko, sine die, leg. *Trabandt*, det. *Zapałowicz* (12.02.1908)" – KRAM! (132292). – [*Aconitum bucovinense* Zapał.].

Aconitum napellus var. *carpathicum* Zapał. in Rozpr. Wydz. Mat.-Przyr. Akad. Umiej., Dział B. Nauki Biol. 48: 84. 1908. Protologue text: „Babia Góra z

niższej dziedziny lasów (*Bobek*), z innego miejsca (*Kulczyński*). Mała Łąka w Tatrach (*Kulczyński*). Lectotype (designated here): „Mała Łąka, 13.08.1875, leg. et det. W. Kulczyński” – KRAM! (132272). Other syntype: „Babia Góra, ? .08.1876, leg. W. Kulczyński” – KRAM! (132270). – [*Aconitum firmum* Rchb. subsp. *firmum*].

Aconitum napellus var. *czarnohorensse* Zapał. in Rozpr. Wydz. Mat.-Przyr. Akad. Umiej., Dział B. Nauki Biol. 48: 86. 1908. (<http://ipni.org/urn:lsid:ipni.org:names:77062909-1:1.2>). Protologue text: „W Górach Pokucko-Marmaroskich, szczególnie na Czarnej Horze i w Alpach Rodneńskich w krainie kosodrzewu często, najwyżej tam 2010–2030 m; liczne okazy z Czarnej Hory i z Pietrosu w Alpach Rodneńskich (*Zapałowicz*)”. Lectotype (designated here): „Góry Pokucko-Marmaroskie, Pietrosz, 8.08.1880, leg. et det. H. Zapałowicz” – KRAM! (246853). Other syntypes: (1) „Pietrosz Kr. Kos., 25.07.1905, H. Zapałowicz” – KRAM! (132297); (2) „Góry Pokucko-Marmaroskie, leg. et det. H. Zapałowicz, 28.07.1880” – KRAM! (246854); (3) „Czarna Hora, 18.09.1881, leg. et det. H. Zapałowicz (12.02.1908)” – KRAM! (132277). – (≡ *Aconitum czarnohorensse* (Zapał.) Mitka).

Aconitum napellus f. *glabratum* Zapał. in Rozpr. Wydz. Mat.-Przyr. Akad. Umiej., Dział B. Nauki Biol. 48: 87. 1908. Protologue text: „Ihrowiszcze (*Zipser*), Howerla (*Witwicki*), Pietrosu na Piatra alba (*Zapałowicz*), Dorna Watra na Bukowinie (*Rehman*). Lectotype (designated here): Góry Pokucko-Marmaroskie, Pietrosz, 29.08.1880, leg. et det. H. Zapałowicz” – KRAM! (246852). Other syntypes: (1) „Ihrowiszcze granica Węgier, ??.1865, leg. S. Zipser” – KRAM! (132255); (2) „Howerla koło Żabiego, ??.1865, leg. Witwicki” – KRAM! (132254); (3) „Dorna Watra na Bukowinie”, sine die, *Rehman*” – KRAM! (132266). – [*Aconitum czarnohorensse* (Zapał.) Mitka].

Aconitum napellus f. *grofense* Zapał. in Rozpr. Wydz. Mat.-Przyr. Akad. Umiej., Dział B. Nauki Biol. 48: 84. 1908. – Protologue text: „W Karpatach nad Łomnicą: p. Kotelec pod Grotą (*Wołoszczak*)”. Lectotype (designated here, or perhaps holotype): „W Karpatach nad Łomnicą: p. Kotelec pod Grotą, 20.07.1889, leg. E. Wołoszczak, det. H. Zapałowicz” – KRAM! (132282). – [*Aconitum firmum* Rchb. subsp. *firmum*].

Aconitum napellus f. *howerlanum* Zapał. in Rozpr. Wydz. Mat.-Przyr. Akad. Umiej., Dział B. Nauki Biol. 48: 87. 1908. Protologue text: „Howerla i z innego szczytu w Czarnej Horze (*Wołoszczak*)”. Lectotype (designated here): „Czarna Hora na Negrowin, 2.08.1888, leg. E. Wołoszczak” – KRAM! (132276a). Other syntype: „Howerla, 26.07.1886, leg. E. Wołoszczak, em. H. Zapałowicz” – KRAM! (132269). – [*Aconitum czarnohorensse* (Zapał.) Mitka].

Aconitum napellus f. *latisectum* Zapał. in Rozpr. Wydz. Mat.-Przyr. Akad. Umiej., Dział B. Nauki Biol. 48: 84. 1908. – Protologue text: „Mała Łąka w Tatrach (*Kulczyński*)”. Lectotype (designated here, or perhaps holotype): „Mała Łąka, 13.08.1875, leg. W. Kulczyński” – KRAM! (132257), first synonymized by Mitka 2003. – [*Aconitum firmum* Rchb. subsp. *firmum*].

- Aconitum napellus* var. *lomnicense* Zapał., Rozpr. Wydz. Mat.-Przyr. Akad. Umiej., Dział B. Nauki Biol. 48: 87-88. 1908. Protologue text: „W Karpatach Wschodnich: nad Łomnicą „przy stawie Grofy” (*Woloszczak*), więc już dość nisko, mniej więcej w dziedzinie górskiej”. Lectotype (designated here, or perhaps holotype): „Przy stawie Grofy, 31.08.1890, leg. *E. Wołoszczak*, det. *H. Zapałowicz* (16.02.1908)” – KRAM! (132286). – [*Aconitum nanum* (Baumg.) Simonk.].
- Aconitum napellus* f. *minimum* Zapał. in Rozpr. Wydz. Mat.-Przyr. Akad. Umiej., Dział B. Nauki Biol. 48: 87. 1908. Protologue text: „Na Czarnej Horze: Pop Iwan koło 2000 m (*Zapałowicz*)”. Type not designated (no material traced). – Identity uncertain.
- Aconitum napellus* f. *puberulum* Zapał. in Rozpr. Wydz. Mat.-Przyr. Akad. Umiej., Dział B. Nauki Biol. 48: 84-85. 1908. Protologue text: „Babia Góra w lasach pod Djablakiem koło 1160 m (*Zapałowicz*)”. Lectotype (designated here, or perhaps holotype) „1160 m, 24.07.1906, *H. Zapałowicz*” – KRAM! (132299), first synonymized by Mitka 2003. – [*Aconitum firmum* subsp. *moravicum* Skalický].
- Aconitum napellus* f. *rodnense* Zapał. in Rozpr. Wydz. Mat.-Przyr. Akad. Umiej., Dział B. Nauki Biol. 48: 87. 1908. Protologue text: „W krainie kosodrzewu Alp Rodneńskich, widocznie przeważnie lub wyłącznie na wapieniach: Piatra rei 1300-1400 m, Galacz 1760-1850 m (*Zapałowicz*)”. Lectotype (selected here): „Alpy Rodneńskie, Galacz, 15.08.1907, leg. et det. *H. Zapałowicz*” – KRAM! (132301). Other syntype: „Piatra Alpy Rodneńskie, 15.08.1907, leg. et det. *H. Zapałowicz*” – KRAM! (132302). – [*Aconitum czarnohorensse* (Zapał.) Mitka].
- Aconitum napellus* var. *silesiacum* Zapał. in Rozpr. Wydz. Mat.-Przyr. Akad. Umiej., Dział B. Nauki Biol. 48: 84. 1908. Protologue text: „Barania w Karpatach u źródeł Wisły na Śląsku (*Woloszczak*)”. Lectotype (designated here, or perhaps holotype): „Na Baraniej Górze w Beskidzie, okoł. 1000 m, Galicya, 10.07.1895, leg. *E. Wołoszczak*, 13.07.1908, rev. *H. Zapałowicz*” – KRAM! (132291), first synonymized by Mitka 2003. – [*Aconitum firmum* subsp. *moravicum* Skalický].
- Aconitum napellus* f. *subincisum* Zapał. in Rozpr. Wydz. Mat.-Przyr. Akad. Umiej., Dział B. Nauki Biol. 48: 86-87. 1908. – Protologue text: „Ukiernia w Karpatach na górnym porzeczu Łomnicy (*Woloszczak*)”. Lectotype (designated here, or perhaps holotype): „Na północno-zachodnim szczycie Ukierni przy Łomnicy, Karpaty, 01.08.1890, *E. Wołoszczak*” – KRAM! (132285). – [*Aconitum czarnohorensse* (Zapał.) Mitka].
- Aconitum napellus* f. *turkulense* Zapał. in Rozpr. Wydz. Mat.-Przyr. Akad. Umiej., Dział B. Nauki Biol. 48: 86. 1908. Protologue text: „W krainie kosodrzewu Czarnej Hory pod Turkułem (*Zapałowicz*)”. Lectotype (designated here, or perhaps holotype): „Czarna Hora, 21.08.1880. *H. Zapałowicz*, det. *H. Zapałowicz* (12.02.1908)” – KRAM! (132278), first synonymized by Mitka (2003). – [*Aconitum czarnohorensse* (Zapał.) Mitka].
- Aconitum napellus* f. *subfissum* Zapał. in Rozpr. Wydz. Mat.-Przyr. Akad. Umiej., Dział B. Nauki Biol. 48: 85. 1908. – Protologue text: „Kościeliska w Tatrach (*Krupa*)”. Lectotype (designated here, or perhaps holotype): „Kościelisko, Tatry, sine die,

- Krupa*” – KRAM! (132284). – [*Aconitum firmum* Rchb. subsp. *firmum*; first synonymized by Mitka (2003)].
- Aconitum napellus* var. *subtatrense* Zapał. in Rozpr. Wydz. Mat.-Przyr. Akad. Umiej., Dział B. Nauki Biol. 48: 83–84. 1908. Protologue text: Tatrzy, w strefie widocznie niższej, podalpejskiej, okazy zebrane przez *Berdaua*, *Rehmana* i *Jabłońskiego*, bez bliższego oznaczenia miejscowości. Lectotype (designated here): „Widoczne z Tatr, *Berdau*” – KRAM! (132287). Other syntypes: (1) „Widoczne z Tatr, sine die, leg. *A. Rehman*, det. *H. Zapałowicz* (12.02.1908)” – KRAM! (132268); (2) „Czarna Hora, najprędzej Tatrzy, *H. Zapałowicz*” – KRAM! (132265); (3) Tatrzy wszędzie prawie, ?.07.1862, *W. Jabłoński*” – KRAM! (132289). – [*Aconitum firmum* Rchb. subsp. *firmum*].
- Aconitum napellus* f. *subvestitum* Zapał. in Rozpr. Wydz. Mat.-Przyr. Akad. Umiej., Dział B. Nauki Biol. 48: 85. 1908. Protologue text: „Szypcy w Czarnej Horze (*Ślędziński*)”. Lectotype (designated here, or perhaps holotype): „Czarna Hora, Szypcy, 21.08.1875, leg. *Ślędziński*” – KRAM! (132260). – [*Aconitum czarnoborensse* (Zapał.) Mitka].
- Aconitum napellus* var. *swidovense* Zapał. in Rozpr. Wydz. Mat.-Przyr. Akad. Umiej., Dział B. Nauki Biol. 48: 85. 1908. Protologue text: „Na północny-zachód od Czarnej Hory w Górach Swidowskich: Dragobrat. Bliźnica 1700 m i t. d. (*Zapałowicz*)”. Lectotype (designated here, or perhaps holotype): „G. Świdowskie, Dragobrat, Bliźnica, 10.08.1882, leg. et det. *H. Zapałowicz*” – KRAM! (132385). – [*Aconitum czarnoborensse* (Zapał.) Mitka].
- Aconitum napellus* var. *tatrense* Zapał. in Rozpr. Wydz. Mat.-Przyr. Akad. Umiej., Dział B. Nauki Biol. 48: 86. 1908. Protologue text: „Okazy ze Świnicy (*Kotula*) i z innego miejsca w Tatrach (*Janota*). Według *Kotuli* (l.c.) w krainie kosodrzewu Tatr w ogóle bardzo często, sięga po 2180–2210 m”. Lectotype (designated here): „Tatrzy (?), ??.1877, leg. Dr. *E. Janota*, det. *Zapałowicz*” – KRAM! (132261). Other syntype: „Tatrzy pod szczytem Świnicy, 30.07.1880, det. *H. Zapałowicz* (12.02.1908)” – KRAM! (132279). – [*Aconitum firmum* Rchb. subsp. *firmum*].
- Aconitum napellus* f. *tenuisectum* Zapał. in Rozpr. Wydz. Mat.-Przyr. Akad. Umiej., Dział B. Nauki Biol. 48: 86. 1908. Protologue text: „Dział między Howerlą a Pietroszem, blisko drugiego na skałkach jurajskich koło 1550 m (*Zapałowicz*)”. Lectotype (designated here, or perhaps holotype): „Czarna Hora, Pietrosz, 5.08.1906, leg. et det. *H. Zapałowicz*” – KRAM! (132298), first synonymized by Mitka 2003. – [*Aconitum czarnoborensse* (Zapał.) Mitka].
- Aconitum napellus* f. *vestitum* Zapał. in Rozpr. Wydz. Mat.-Przyr. Akad. Umiej., Dział B. Nauki Biol. 48: 85. 1908. – Protologue text: „Pilsko, widocznie z krainy kosodrzewu (*Krupa*), 2 okazy”. Lectotype (designated here, or perhaps holotype): „Pilsko, ?.08.1878, leg. *Krupa*” – KRAM! (132283), first synonymized by Mitka 2003. – [*Aconitum firmum* subsp. *moravicum* Skalický].
- Aconitum napellus* f. *zeleminum* Zapał. in Rozpr. Wydz. Mat.-Przyr. Akad. Umiej., Dział B. Nauki Biol. 48: 87. 1908. Protologue text: „Karpaty na południe od Skolego: Zelemin, Wysoka-Ihrowiszczce (*Woloszczak*)”. Lectotype (designated here): „Pod szczytem

Wysokiej (Ihrowiszcze) w okolicy Łomnicy, Karpaty, 27.07.1889, leg. *E. Wołoszczak*, det. *H. Zapałowicz* – KRAM! (132280). Other syntype: „Zełemin, ?08.1891, *E. Wołoszczak*” – KRAM! (132288). – [*Aconitum czarnoborense* (Zapał.) Mitka].

Discussion

In 1907 Zapałowicz started to lay down his *opus magnum*, “Conspectus florae Galiciae”. As detailed by Stafleu and Cowan (1988: 521), this work was first published in fascicles in the “Rozprawy” (e.g., Zapałowicz 1908a), under its alternative Polish title “Krytyczny Przegląd Roślinności Galicji” (“Przegląd”). In total, from 1907 to 1914 thirty fascicles were published. Fascicles 1–22 were subsequently reprinted and published in book form in three volumes. Volume 1 consisting of fascicles 1–7, was published in 1906; volume 2 (Zapałowicz 1908b), comprising fascicles 8–14, in 1908; and volume 3, with fascicles 15–22, in 1912. Fascicles 23–30, which were published in 1912–1914, were not reprinted in book form.

In order to establish the effective date of publication of the “Przegląd” and volume 2 of “Conspectus florae Galiciae” in which the treatment of *Aconitum* is published, the first author checked the available documents in the archives of the library of the Institute of Botany of the Polish Academy of Sciences (*Polska Akademia Nauk*, PAN) (1), the Academic Library of the Academy of Sciences and Letters (*Polska Akademia Umiejętności* PAU) (2), the Archives of the Science of the PAN and PAU (3), the Jagiellonian University Archives (4) and the Jagiellonian Library (5).

Each fascicle of the “Rozprawy” was published subsequent to a meeting of the Division of Mathematics and Natural Sciences of PAU. At the end of each year, the fascicles of were put together and issued as an annual volume (“Przegląd”) with its own title page and table of contents. Unfortunately wrappers mostly removed front pages and tables of content from individual fascicles. In the Jagiellonian Library in Cracow (ID number 28061 III) we found a single vol. 48 of the “Rozprawy” fascicles with the original front and back wrapper sheets of the fascicles have been preserved. Three “Rozprawy” fascicles were published in 1908. The first, with seven articles, includes parts XII and XIII of the “Przegląd”; the second contains nine articles and the third and last, six. Part XII of the “Przegląd” was presented to the Division of Mathematics and Natural Sciences at its meeting on 2 March 1908; the minutes of the meeting on 4 May 1908 state that part XIII was approved and sent to the printers. On the following day (5 May) the Jagiellonian University Printing House billed PAU for the first fascicle of the “Rozprawy”, in which both parts are included. The bill for the second fascicle is dated 7 August 1908; that for the third fascicle, 22 December 1908. The word „wydrukowano” [printed] appears on all bills, so that the date of effective publication of parts XII and XIII of “Przegląd” may be accepted to be 5 May 1908. The Jagiellonian Printing House billed PAU for volume 2 of the “Conspectus” on 22 December 1908. Effective publication of the *Aconitum* names in question took place on the earlier date.

Acknowledgements

We are indebted to Ryszard Ochyra and Walter Greuter for valuable comments on the manuscript; to Piotr Köhler for help in searching the archives of the Polish Academy of Sciences and Letters; and to Jacqueline M. Beacham (New Mexico State University, Las Cruces) for checking the English.

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